A study of the affects of Habitat fragmentation on the woodland edge microclimate and on the structure and composition of woodland ground flora

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A Study of the Affects of Habitat Fragmentation on the Woodland Edge Microclimate and on the Structure and Composition of woodland Ground Flora.

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Abstract

A study of the affects of habitat fragmentation on the microclimate and ground flora at the edge of an area of secondary woodland was conducted. Vegetation was sampled in an array of 60 quadrats arranged in transects running parallel with the edge of the woodland and at increasing distances from it. Species abundance at each quadrat was measured using the Domin scale. Point quadrats were used to allow assessment of vegetation structure and canopy cover at each quadrat was described using a point centred quarter method. Environmental variables including illumination, P.A.R., soil temperature, air temperature, soil moisture, soil organic content and pH were measured at each quadrat.

Data was analysed using a variety of univariate and multivariate statistics. Results indicated a microclimatic and vegetational 'transition zone' of approximately 10 metres in diameter at the northern boundary of Moorhouse Wood and adjacent habitats. This was indicated by; 1. Illumination, P.A.R., soil and air temperature, soil moisture and soil organic content all underwent significant alterations over this distance and continued to change more gradually further into the wood. 2. Edge oriented patterns of variation were found in both canopy and ground floral community composition and in general, species with ecological preferences for disturbed or for warm and light conditions were increased in abundance at the edge of the woodland. Some evidence of invasion by non-woodland species was found but these did not appear to be colonising the woodland interior. 3. Ground vegetation structure was altered by proximity to the woodland edge. This was shown to be unrelated to most microclimatic variables and it is suggested that a high level of disturbance is more likely to be responsible for the decreased height of vegetation at the boundary.

Comments are made concerning the significance of these findings and their importance in understanding the affects of habitat fragmentation on the woodland microclimate and ground flora.

Acknowledgements

I would like to express my gratitude to Dr. Phil Gates, Dr. Brian Huntley and Dr. Phil Hulme for all of their support and advise throughout this project. I would also like to thank Dr. Val Standon for the information she provided about Moorhouse Wood and all the other people who lent a hand whenever it was needed.

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1.0 Introduction

Vegetation at deciduous woodland margins in the Northern Hemisphere is often clearly distinct from that of the woodland interior (Matlack 1994). Both in their structure and composition, all levels of vegetation frequently exhibit striking changes where they are exposed to microclimatic gradients and therefore the changes in resource availability, which exist over the boundary between fragmented woodland and surrounding habitats. This phenomenon has been widely studied in many types of forest and woodland ecosystems (Matlack 1994, Laurance 1991, Williams-Linera 1990), however it has often been the case that these studies have focused primarily on the ~~a~~effect of edge creation on woody species and particularly the canopy (Wales 1972). A large number of different factors affect the way in which an area of woodland may respond to the creation of an artificial edge due to for example, the spread of agriculture or urban development. This study concentrates on the investigation of just one such woodland edge and still further on its herbaceous ground flora. Whilst it will therefore be impossible to construct any generalisations from the results of this study, it is intended that as full a picture as possible of the ~~a~~effect of past fragmentation on the ground flora of this small area of woodland may be produced.

Throughout much of the world, both in tropical and temperate regions, the majority of our woodlands and forests have become fragmented and isolated due to increasing human development (Laurance 1991). Today in an attempt to preserve what remains of these ecosystems, reserves have been created. It has long been a matter of contention however as to the extent these isolated fragments can sustain a representative biota (Laurance 1991). The theory of Island biogeography (MacArthur and Wilson 1967) has, in the past, been applied to the behaviour of these fragments and serves to some extent to explain why population dynamics within an isolated woodland area are fundamentally altered. Just as on an island, gene flow between populations of species confined to woodland ecosystems is restricted. Unlike an island however, an area of fragmented woodland is usually surrounded by modified habitats which contain components capable of invasion into the woodland, particularly as environmental conditions at the woodland boundary are often affected in the invader's favour.

In order to protect and conserve diminishing woodland and forest areas it is extremely important to establish amongst other things; 1. how and to what extent vegetational composition and structure of a woodland area alters from the boundary to the interior and 2. whether this is related in any way to microclimatic changes caused by the influence of adjacent conditions. Although many studies of this type have been completed in the past, there has been a conspicuous lack of agreement in the details of such factors as; width of the microclimatic transition zone at the woodland/field boundary, relative importance of particular microclimatic features and the extent of invasion by generalists from other communities (Matlack 1993). Equally there has been a particular lack of information concerning the role of the 'edge effect' in the ecology of forest herbs and the ground floral community as a whole (Dunne and Pickett 1985).

Those studies which have been completed have shown that the picture of environmental and plant community changes at a woodland or forest edge is very complex. As most of our pristine forest ecosystems now survive only in the tropics, this is where most work in this area has been completed. In 1990 Williams-Linera published the results of a major study of vegetation structure and environmental conditions of forest edges in Panama. This study reported, amongst other effects, an increase at the boundary in solar radiation, air temperature, wind velocity and rainfall reaching the soil in comparison to the forest interior, it also reported a decrease in humidity at the boundary. Most of these microclimatic changes however were found only up to 15 metres into the forest. Vegetation structure was found to be altered at the boundary where there was an increased density of trees of < 10 cm in diameter and where the canopy was found to be most open. In 1991 Laurance reported similar environmental changes, however in stark contrast to the Williams-Linera study (1990), where no evidence of compositional change was reported, this author demonstrated an elevated abundance of light loving and pioneer species at the forest boundary. Other studies have disagreed with the environmental data presented by both these authors and reported microclimatic changes up to 40 metres into forest areas (Matlack 1993). Despite their differences, most studies agree that fragmentation is likely to have more serious consequences in temperate climates than in the tropics. In complex tropical ecosystems resistance to alteration is high and regrowth of vegetation at the boundary is rapid, decreasing the chance of a significant shift towards non-rainforest vegetation. Less complex deciduous ecosystems are believed to be more susceptible to invasion and are slow to replace damaged vegetation at the boundaries.

Many studies completed in the Northern Hemisphere have agreed with the above hypothesis to some degree however, most have been equally ambiguous in their results. Some studies reported microclimatic alterations up to 50 metres into a woodland (Matlack 1993) whereas others found alterations only up to 20 metres from the edge (Wales 1972). Behaviour of a woodland ecosystem at any particular time and as a result of the creation of an artificial edge will often differ depending upon numerous variables including time since creation, level of disturbance, orientation and size of the fragment (Janzen 1983). These and other variables may have important and significant affects and are often responsible for much of the disagreement between reports. Studies completed in deciduous woodlands have frequently demonstrated much greater 'edge effects' on a south facing and therefore more sunny edge than on a North facing one (Wales 1972). Equally a younger edge which has had little time for regrowth is characterised by much steeper environmental gradients across the boundary and is likely to show stronger vegetational gradients (Matlack 1994).

In general many of the responses of woodland vegetation to fragmentation in the temperate region appear similar to those in the tropics i.e. higher densities of saplings and shrubs on the woodland margins and a more open canopy (Wales 1972, Matlack 1994). There is very little information however to indicate how ground floral composition and structure might be effected on the edge of a woodland fragment. In the past some authors have found substantial alterations in species composition at the woodland edge, with the presence of greatly increased numbers of shade intolerant species (Wales 1972). Some have suggested that this is due to invasion of species more typical of open habitats and have reported differing composition, density and form of vegetation on borders (Gysel 1951). Others have found no species present at the edges of a woodland which are not present in the interior and thus believe that the edge offers no opportunity for colonisation from the outside (Matlack 1994). Once again the affects of the creation of an artificial edge on ground vegetation seem likely to vary considerably with each individual case due to the large numbers of influencing factors.

In the British Isles most of our woodland areas are no longer original ancient woodland. This study concentrates on an area of secondary woodland and aims to establish the fundamental patterns of variation within the ground vegetation and it's microclimate, which may be associated with distance from the edge of the woodland. No comparison is made with other sites due to the short duration of the study and therefore no comment is made concerning the affects of orientation or age of the edge. The aim of this study is simply to provide an in-depth picture of the ~~a~~effects of this particular edge on the woodland ground flora, it~~'~~s microclimate and their interaction.

2.0 Site Description

The study was conducted in an area of woodland situated between Durham and Sunderland (NZ310460) known as Moorhouse Woods (see fig 2.1).

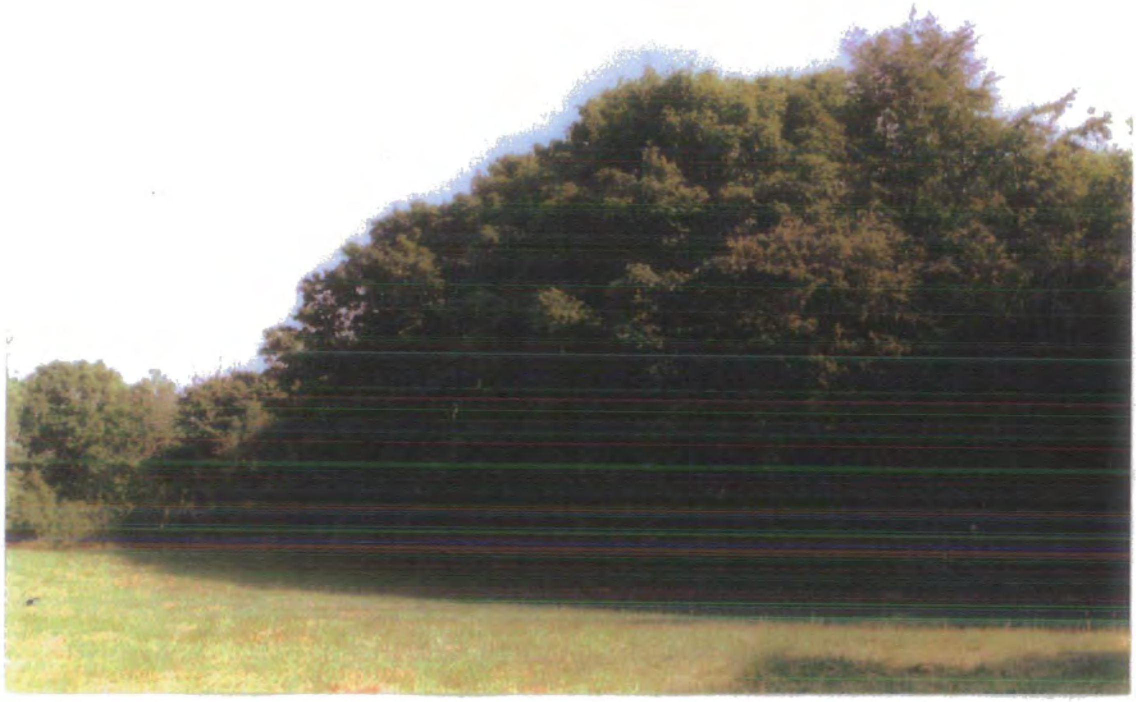
The woodland was selected partially due to its convenient position, but primarily because its northerly edge provided the most suitable site for a study of this kind in the vicinity of Durham.

The woodland covers an area of approximately 8.3 ha and is roughly square in shape. The area is bordered on three sides by arable farmland and on the fourth, (used in this study), by closely grazed pasture.

The site is owned by the National Trust and leased to the Durham Wildlife Trust. The history of the area is therefore fairly well documented. Today the site contains semi-natural mixed deciduous woodland believed to have been planted in the eighteenth century on an ancient woodland site, however the documented history of the site extends as far back as the sixteenth century. The woodland site would originally have been part of the Rainton Park and Mallygill wood complex but was cut off from these riverine areas by the construction of the A1(M). Moorhouse wood is said to be shown on a map of 1570 and its boundary appears on Armstrong's map of 1776. On the Tithe Plan of 1846 the area is shown as partly wood and partly plantation. Evidence that mining has occurred in the woods at some point is found on a map of 1896 which shows an old coal pit. The woodland is now believed to be suffering some subsidence. The remains of a building, a coal washing pit and a mine shaft are found on the east corner of the wood.

During the Second World War the majority of the woodland was felled but was later partially replanted and partially left to regrow from cut stumps. The current northerly edge, used in this study, has therefore been present for at least the past 40-50 years.

Figure2.1 Photographs of the Northern edge of Moorhouse wood.



Geologically the area is described as coal measure shale overlain by boulder clay. At least one small gill runs through the wood cutting through shale and exposing coal seams although this dries up in the summer. Two public footpaths also cross the woodland and the area is well used by local people although it is not believed that illegal felling in a major problem.

Biologically the canopy is dominated over much of the area by *Quercus petraea* (sessile oak), although a wide variety of other species occur including *Acer pseudoplatanus* (sycamore), *Ulmus procera* and *U. glabra* (elm and wych elm) , *Fraxinus excelsior* (ash), *Fagus sylvaticus* (beech), *Castanea sativa* (sweet chestnut), *Crataegus monogyna* (hawthorn) and *Carpinus betulus* (hornbeam). Understorey species include *Ilex aquifolium* (holly), *Corylus avellana* (hazel), *Crataegus monogyna* (hawthorn), *Sambucus nigra* (elder) and some *Malus sylvestris* (crab apple). Ground floral species, the subject of this study, are varied and include *Mercurialis perennis* (dog's mercury), *Anemone nemorosa* (wood anemone), *Galium odoratum* (sweet wood ruff), *Chrysosplenium oppositifolium* (opposite leaved golden saxifrage), *Oxalis acetosella* (wood sorrel), *Viola riviniana* (dog violet), *Geum urbanum* (wood avens), *Geranium robertianum* (herb robert) and *Veronica montana* (wood speedwell). Despite this wide variety of ground floral species, disturbance in the wood continues at a constantly high level and thus, as with many semi-natural woodlands, the ground vegetation is dominated by only a few species including *Rubus fruticosus* (bramble), *Hedera helix* (ivy) and *Milium effusum* (wood millet).

The study site was chosen due to its suitable length and the fact that unlike so many other woodland edges bordering farm land, it had not been completely embedded by the planting of *C. monogyna* bushes. Within the bounds of this study it was obviously necessary that any edge used should be as natural as possible.

Most of the information in this site description was provided by Dr. Val Standen (chairperson of the reserve management committee) in a document produced in 1993.

3.0 Materials and Methods

All field work was conducted in the period from the beginning of June, when the canopy was considered to be fully developed, until mid July. It has been demonstrated that even in the winter, a northern hemisphere deciduous canopy can reduce light levels incident upon the ground flora by up to 30% (Matlack 1993) and probably affect other environmental variables equally. Despite this it was felt that the study would be most successful in exposing any edge orientated patterns in the ground flora if conducted when there was maximum contrast in environmental conditions between the edge of the woodland and the interior, i.e. after canopy closure. Whether the environmental conditions at this time of year are of either equal or greater importance to ground flora performance than those at other times is discussed later. It was not possible however to establish, within the scope of this study, the annual patterns of environmental change in this woodland or their ecological significance. It is therefore assumed that environmental conditions measured are responsible for patterns found in the vegetation.

Prior to vegetation sampling, the site was explored on foot and a species list compiled. Both at this time and during vegetation sampling all vascular plants and bryophytes found were identified to species level where possible. Vascular plants were mostly identified in the field using Clapham, Tutin and Moore (1987), bryophytes were mainly returned to the lab for identification using Smith (1978). Many species which would have been more difficult to identify earlier in the year were in flower and presented no difficulties, however some such as the Willow herbs which had yet to flower were recorded simply as *Epilobium* spp. Microspecies of *Rubus fruticosus* and *Rosa canina* were not separated. Nomenclature of all higher plants follows Clapham et. al. (1987). Bryophyte nomenclature follows Smith (1978).

The study site consisted of an array of sixty 1 x 4 m quadrats giving each quadrat an area of $4m^2$, that generally regarded as sufficient to be representative of the woodland ground floral community (Rodwell 1991, Mueller-Dombois and Ellenberg 1974)). Quadrats were arranged in six transects running parallel to the edge of the woodland and at 0, 5, 10, 20, 40 and 60 metres from it. The ten quadrats within each transect were placed at 10 metre intervals and were rectangular, as opposed to square, so that close to the edge of the woods, quadrats in adjacent transects were as widely spaced as possible.

3.1 Vegetation Sampling

At each quadrat several measures of the vegetation both in and around the quadrat were taken. A species list was constructed and abundance of each species was quantified using the Domin scale (table 3.1). All shrubs over 0.5 metres high, within a 1 x 8 m area centred on each quadrat, were identified and noted. The canopy in the vicinity of each quadrat was described using a point centred quarter method (Cottam et. al. 1953). This technique divides the area around the central point of the quadrat into four equal segments using the cardinal points of the compass. The nearest tree to the central point in each quarter is then identified and its distance from that point (in metres) plus its girth at breast height (1.5m from the ground) are measured.

Table 3.1 The Domin scale of species abundance.

The Domin Scale	% Cover
1	< 4%, 1 or 2 individuals
2	< 4%, a few individuals
3	< 4% numerous individuals
4	4 - 10 %
5	10 -25 %
6	25 - 33 %
7	33 - 50 %
8	50 - 75 %
9	75 - 90 %
10	90 - 100 %

In order to gain an insight into the structure of the vegetation at each quadrat 20 point quadrats were also positioned, equally spaced, within the boundaries of each 1 x 4 m quadrat. The structure of the vegetation at each point quadrat was recorded by placing a pole marked in centimetre divisions into the vegetation and noting the height of every touch up the pole and the identity of the touching species.

3.2 Environmental Measurements

For each quadrat seven environmental variables were measured. Soil moisture content, soil organic content and pH measurements were made from a single soil sample taken from the top 10 cm of soil in the centre of each quadrat. All soil samples were taken on the same day to eliminate possible problems arising due to rainfall etc. The soil was weighed, ready for oven drying and pH readings were taken, on the same day as collection. This was intended to ensure no alterations in these variables had occurred by the time measurements were made. After the removal of plant material and mixing with an approximately equal volume of distilled water, the pH of each soil sample was measured using a standard glass electrode pH meter. To determine soil moisture content, soil samples were dried in an oven at 80^{o}c for 48 hours then re-weighed. To determine soil organic content samples were ashed in a muffle oven at 650^{o}c for 2 hours.

The other environmental variables considered were illumination, PAR and air temperature at the level of the ground vegetation and also soil temperature in the top 5 cm of the soil. On four sunny and four cloudy days during the period from the beginning to the middle of July, all four variables were measured at the same time, at each quadrat, at some point between 12 a.m. and 2 p.m. Each variable was therefore measured eight times at each quadrat. Illumination and P.A.R. were measured using a Macam quantum radiometer/photometer model Q101. Air and soil temperature were measured using an Ebsero temperature meter. In analysis, the average of 'sunny day' means and 'cloudy day' means were used for these variables to give a representative measure of their average value throughout the summer. Had it been possible, measurements of red and far red light would also have been acquired to give some indication as to how the quality of light changed with distance from the edge of the woodland, unfortunately the necessary equipment was not available.

3.3 Analysis

Environmental and species data were first analysed with the use of univariate methods including two way analysis of variance and Chi-square tests. Multivariate methods were then employed in the case of some data sets to achieve more detailed results.

3.3.1 Decorana (Detrended correspondence analysis or DCA)

This is an eigenvector ordination technique which extracts the principle axis of variation within the data set (Hill 1979). Although based on reciprocal averaging, it has been refined to avoid the problems of arch distortion and compression at the end of the axis (Hill & Gauch 1980). An ordination diagram is produced, in which similar species or samples are clumped together and dissimilar ones are apart.

3.3.2 Canoco (canonical correspondence analysis or CCA)

This technique is a combination of ordination and multiple regression (Ter Braak 1988). It explains variation in floristic composition by ordination axes that are constrained to be linear combinations of environmental factors. It assumes a response model common to all species and the presence of a single set of environmental gradients to which all species respond. Results are displayed as an environmental bipolt in which the species or samples are ordinated and the environmental variables are represented as arrows. The length and direction of the arrows indicates the degree of their contribution to the patterns exhibited by the principal axes.

4.0 Results

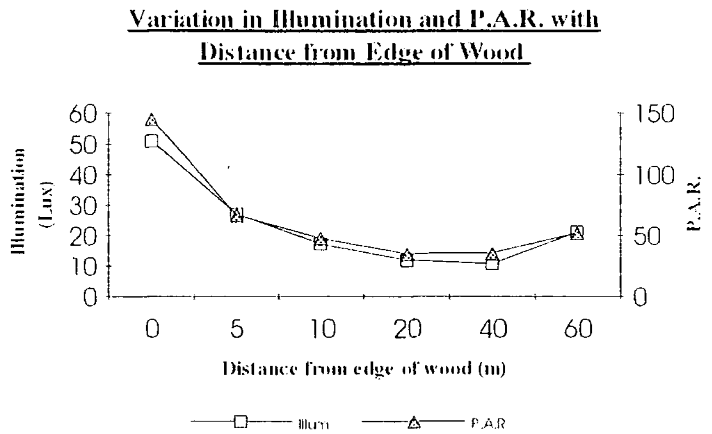
4.1 ~~A~~Effects of Fragmentation on Microclimate at the Edge of the Woodland.

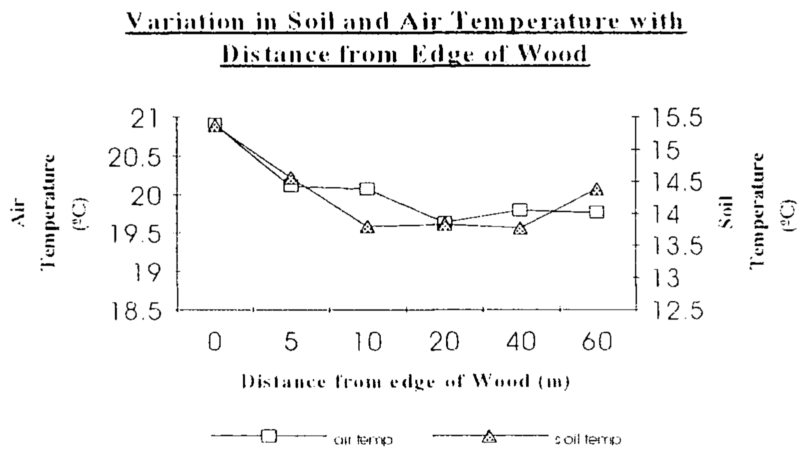
Overall, data collected from seven of the environmental variables, namely P.A.R., illumination, soil temperature, air temperature, pH, soil moisture and soil organic content, indicated some striking changes in environmental conditions with distance from the edge of the wood. Initial correlation of each variable with distance from the edge however, revealed few strong correlation~~s~~, with only air temperature showing a correlation (negative) of greater than 0.5 (tables of environmental measurements and correlation~~s~~ may be found in appendix 1).

Further analysis of the data using two way analysis of variance did indicate significant variation in six of the above seven variables and demonstrated that the apparent lack of correlation with distance was due, in the most case, to the fact that variables did not decrease or increase consistently with distance into the woodland. Instead, the ~~a~~effect of distance on many variables was characterised by a rapid change at the woodland edge followed by stabilisation. Table 4.1 shows probability values generated by the two-way ANOVA, which indicate a highly significant difference in environmental conditions between the transects and therefore with distance into the woodland (variation within each transect was found to be insignificant). Only pH showed no apparent variation attributable to distance from the edge of the wood. Temperature and light reading showed particularly high significance values, demonstrating a very strong trend to decrease with distance from the edge of the woodland. Soil moisture and organic content were also significant in this respect, although to a lesser degree.

Figures 4.1 and 4.2 illustrate the patterns of variation in the above environmental variables with distance from the edge of the woodland. Having established the lack of variation within transects, mean values were used

Figure 4.1 Variation in Environmental variables with distance from the edge of the woodland.





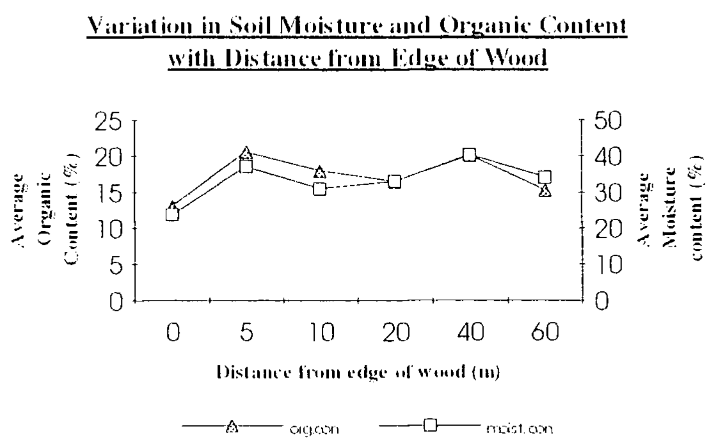
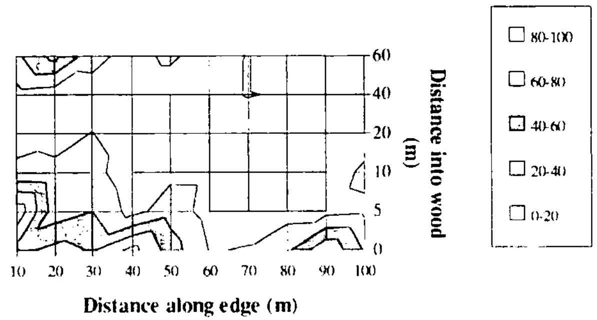
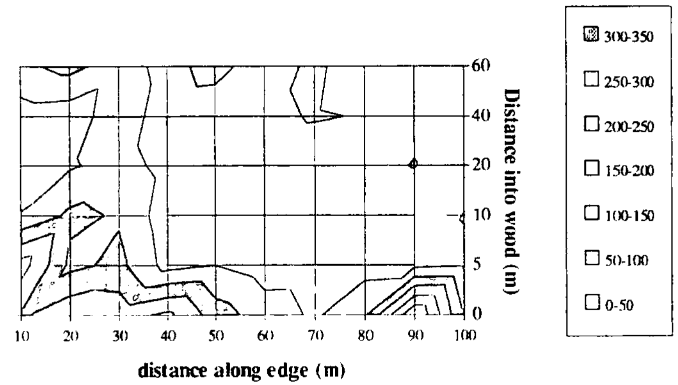


Figure 4.2 Contour diagrams showing variation in environmental variables with distance from edge of wood.

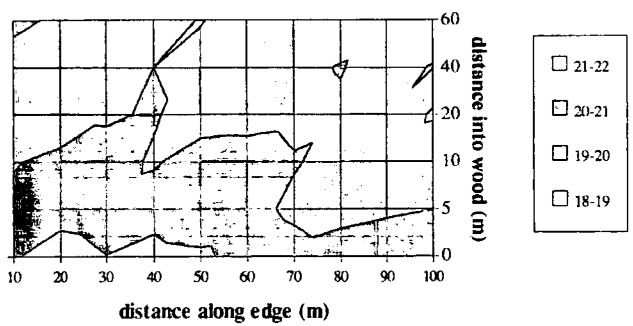
Illumination (Lux)



P.A.R.



Air Temperature (ºC).



Soil Temperature (ºC)

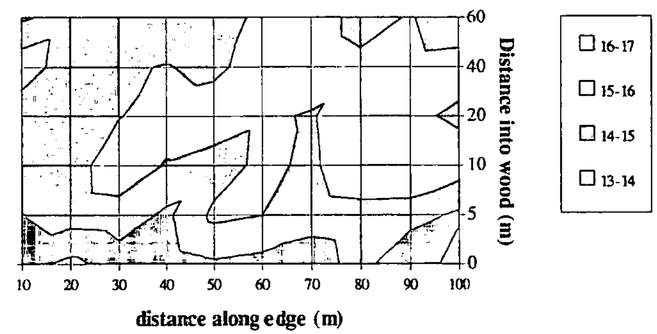
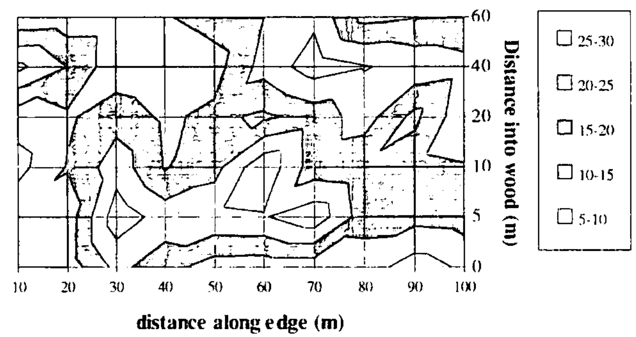
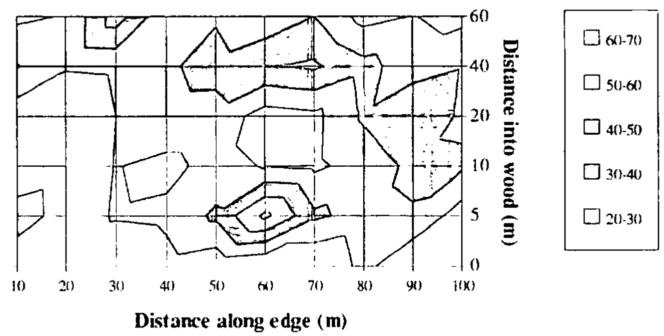


Figure 4.2 Continued

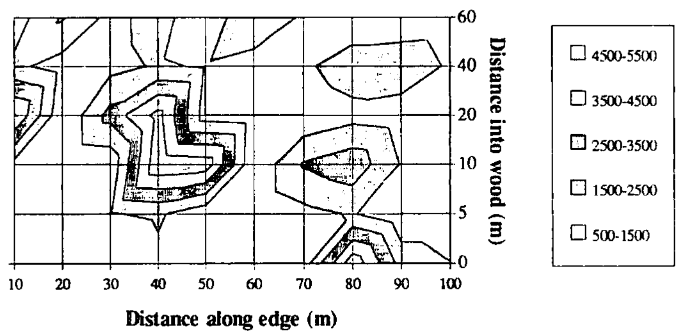
Soil Organic Content (%)



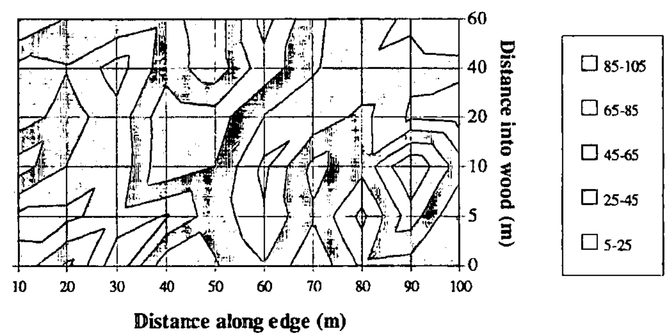
Soil Moisture Content (%)



Tree Density (ha^{-1})



Basal Area ($m^2\ ha^{-1}$)



for the production of these graphs. In the case of illumination and P.A.R., figure 4.1 shows the presence of a transition zone between 0 and 5 metres where there is a sharp decline in the value of these variables. This is followed by a more gradual decrease between 10 and 40 metres. A similar pattern is evident for air and soil temperature although for soil temperature, the transition zone seems to stretch from 0 to 10 metres into the woods. The pattern of variation in soil moisture and organic content with distance from the edge appears to be much less distinct. There is a sharp rise in both of these variables until the 5 metre mark and a slight overall increase in their value from the edge of the woodland to the interior.

Table 4.1 Two-way analysis of variance illustrating significance of variation in environmental variables with distance into the wood.

	degrees of freedom	F value	P value
Illumination	5	7.75	2.49E-05
P.A.R.	5	8.32	1.25E-05
Soil Temperature	5	11.56	3.28E-07
Air Temperature	5	18.52	5.96E-10
Soil Moisture	5	4.87	0.0012
Organic Content	5	3.19	0.015
pH	5	1.25	0.30

need 2 degrees of freedom on each F value

The contour diagrams in figure 4.2 use data from all quadrats as opposed to mean values and illustrate, in detail, the patterns of variation in some of the environmental variables. Again it is clear that many show distinct upward or downward trends particularly in the first 10 metre from the edge of the wood. What is also apparent in both figures 4.1 and 4.2 is the strong correlations which exist between many of the environmental variables themselves (see appendix 1 for details). Illumination and P.A.R. are almost perfectly correlated and correlations also exist between both soil and air temperature and between soil moisture and organic content. Other high correlations, as expected, were air temperature with both illumination and P.A.R. (0.7 and 0.71 respectively) and soil temperature with illumination and P.A.R. (0.58 and 0.56 respectively). Soil temperature was also correlated with soil moisture levels.

Considering that the purpose of this study was to establish the ~~a~~effects of edge altered microclimate on the structure and composition of the ground flora, canopy related variables were also included amongst the environmental conditions which required characterisation. From measurements taken by the point centred quarter method, total basal area (m^2 ha^{-1}) and tree density (ha^{-1}) were calculated for each quadrat (appendix 2). Two way analysis of variance of these values however, demonstrated that neither varied significantly either within or between the transects. Figure 4.2 also demonstrates the lack of any coherent pattern in these variables with distance into the wood

4.2 The ~~A~~Effects of Edge and Edge Related Environmental Variables on Vegetation Composition.

In order to expose patterns of variation within the ground floral composition and any relation these might bear to edge orientated environmental gradients, multivariate analysis techniques were employed. CCA or Canonical Correspondence Analysis was used for this purpose, however prior to this a DCA or Detrended Correspondence Analysis was used with canopy data, in order to extract the dominant patterns of variation within the canopy. Individual species frequency, density and basal area values at each quadrat were used. It was felt that, as variation in total basal area and canopy density alone had proven to be unconnected to distance from the edge of the wood, other more important axes of variation may be extracted in this way. These axes might possibly represent important environmental variables as far as the microclimate of the ground flora was concerned and therefore might be important to include in the CCA.

4.2.1 Detrended Correspondance Analysis

Table 4.2 shows the eigenvalues of the first four principal axes of variation extracted from the canopy data by DCA. From this table it can be seen that the first two axes describe the majority of the variation found.

Table 4.2 Eigenvalues for the 1st Four Principal Axes of the DCA analysis of canopy data.

Axis	Eigenvalue
1	0.859
2	0.527
3	0.389
4	0.280

Figure 4.3 shows a DCA ordination diagram of all samples i.e. quadrats, along the first and second principal axes of variation within the canopy. Sample codes correspond to quadrat numbers i.e. 1-10 equals the transect at the woodland edge, 11-20, at 5 metres from the edge etc. A number of code numbers are deleted for clarity, however a full table of sample scores for the first four axes of the DCA can be found in appendix 4. This diagram also omits three outlying samples which were highly unusual in their canopy composition. Inspection of the ordination diagram in conjunction with ranked species variable scores, also produced for the first four axes by the DCA, gives an indication of the pattern of canopy variation within the samples and therefore whether this is related to distance from the edge.

The first principal axis isolates, at its positive end, quadrats which are dominated by *I. aquifolium*, *C. monogyna* and *F. excelsior* (39, 59 and 60). The cluster towards zero on this axis (54,49,13), is characterised more by *Sorbus aucuparia* (rowan), *Q. petraea* and *C. monogyna*. The majority of quadrats however are not well separated by this axis and are clumped at the lower end. These are characterised by a mixture of common deciduous trees including *Q. petraea*, *C. monogyna*, *A. psuedoplatanus* and *U. glabra* (To make the sample numbers within this group more distinguishable many have been cut out). Although it is not completely clear in figure 4.3, detailed inspection reveals that all but one of the 0 and 5 metre quadrats are found in this cluster.

The second principal axis helps to separate the largest cluster a little more although distinctions are still unclear. At the negative end quadrats containing *Sambucus nigra* (elder) are isolated (40, 21) and at the top of the cluster three groups have begun to develop. Group A are those which amongst other species contain *A. pseudoplatanus*. Quadrats containing *Betula pendula* (silver birch) are found in group B and those in group C and generally dominated by *Q. petraea, C. monogyna* and *U. glabra.*

Figure 4.4 is another ordination diagram of samples, this time using principal axes one and three. Axis 1 describes the same variation as above, Axis three however provides a much higher degree of sample separation. This time at the positive end of the axis, quadrats which contain *Carpinus betulus* (hornbeam) and sometimes *S. nigra* (21, 22, 46) are separated from those which are dominated by the more common combinations of *A. pseudoplatanus, Q. petraea, C. monogyna* etc.. At the bottom of the 3rd axis quadrats are dominated by *C. monogyna* and *A. pseudoplatanus* (8, 9, 43, 45, 25) and in the middle are two groups, quadrats containing *Q. petraea* and *C.monogyna* (32, 38, 53, 50, 35) and those containing *F. excelsior* and *C. monogyna* (58, 56, 42).

The fourth primary axis improved little upon the separation of the samples gained in the first three axes. Quadrats which contained (*Corylus avellana* (hazel) were isolated (32, 38, 55), as were those containing only *Q. petraea* and *A. pseudoplatanus* (4, 6, 7). Overall in terms of distance from the edge of the woodland, very few clear patterns were apparent and it would seem that the canopy is unaffected by proximity to the edge of the wood except in one respect. Whilst it would not be true to say that most *C. monogyna, Q. petraea* and *A. pseudoplatanus* occur along the edge of the wood it would seem to be the case

Figure 4.3 DCA Ordination Diagram

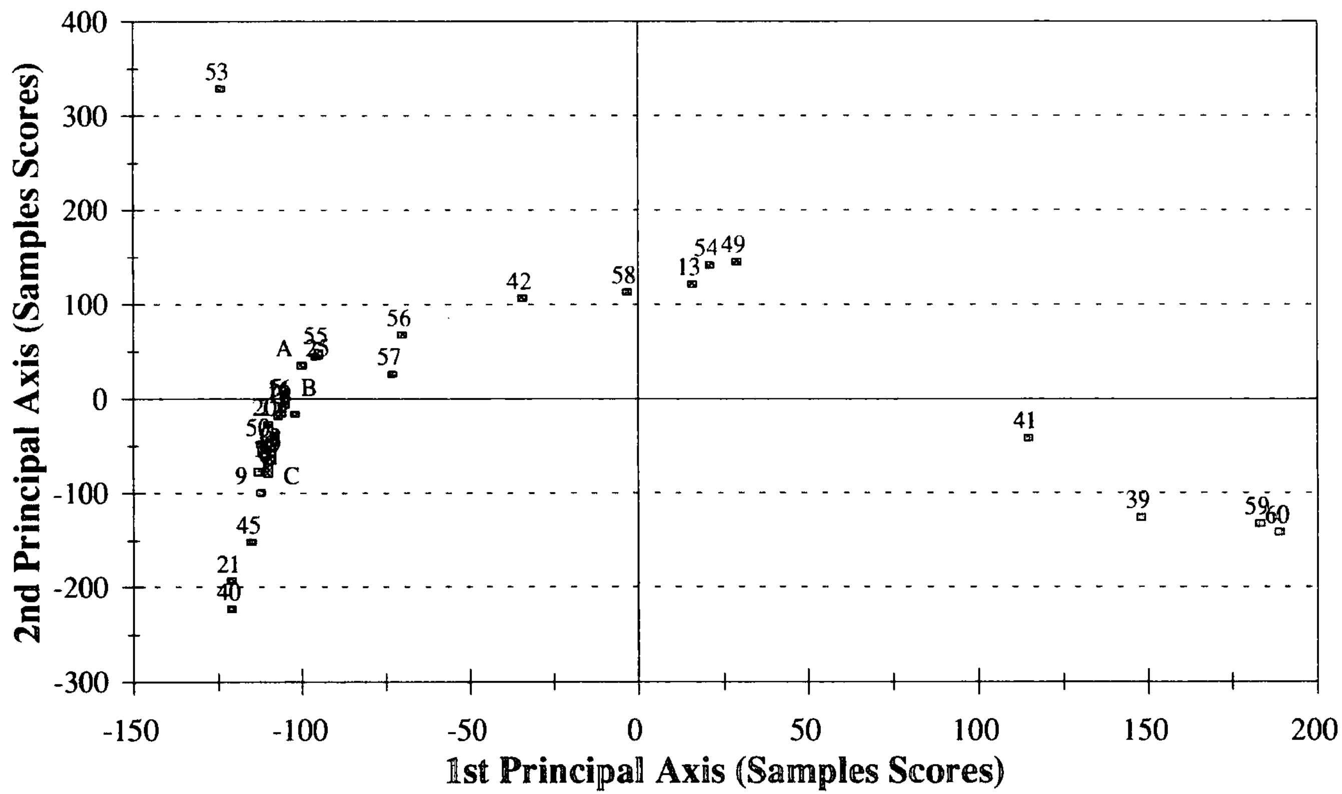
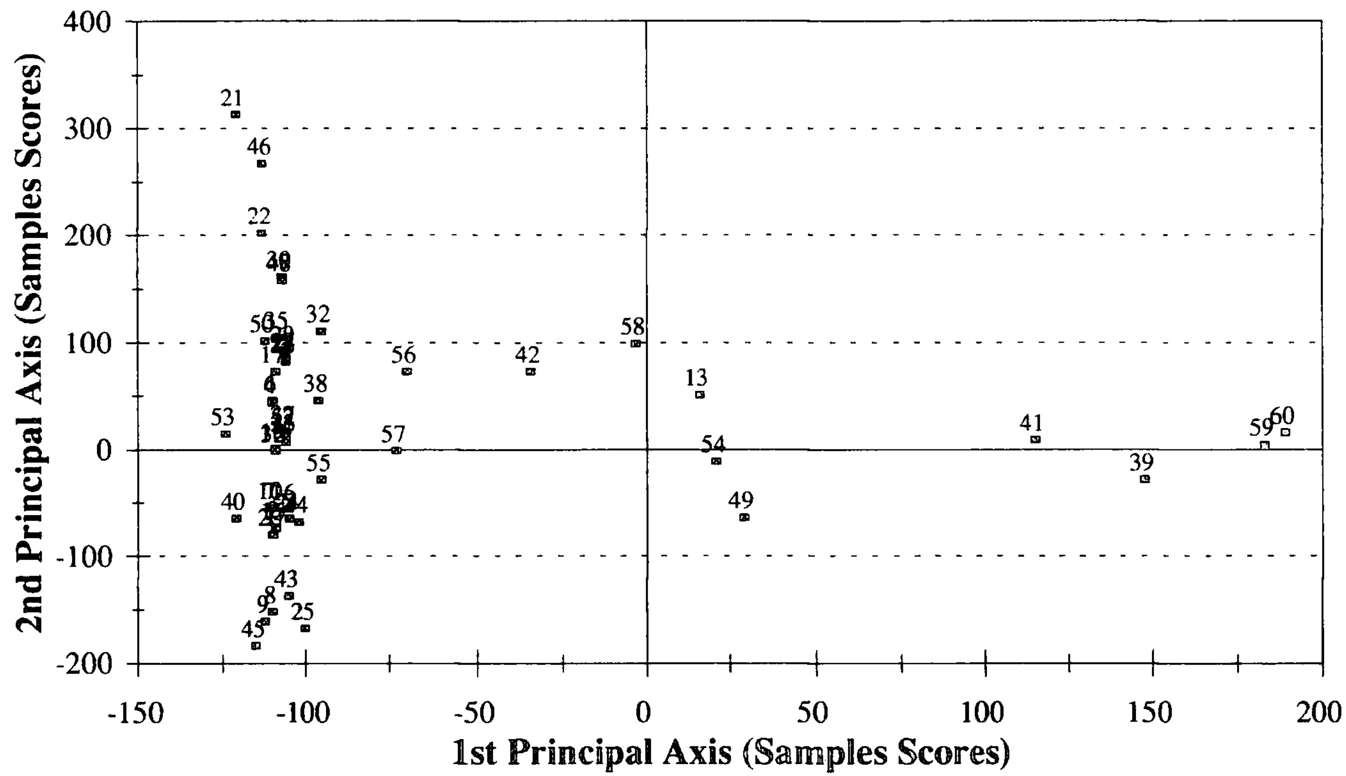


Figure 4.4 DCA Ordination Diagram



that most edge quadrats are dominated by combinations of these trees e.g. 1 and 5 - *C. monogyna* and *Q. petraea*, 4 and 6 - *Q. petraea* and *A. pseudoplatanus*, 8 and 9 - *C. monogyna* and *A. pseudoplatanus*, 7 - *Q. petraea C. monogyna* and *A.pseudoplatanus*. There are no occurrences of *I. aquifolium*, *S. nigra*, *S. aucuparia*, *F. excelsior*, *F. sylvatica*, *C. avellana*, *C. betulus*, *B.pendul*~~*us*~~a or *U. procera* within the first transect, a situation which may reflect these species inability to survive in the transition zone at the edge of a woodland.

The first three principal axes of the DCA were considered to adequately describe the variation in the woodland canopy and were used as additional environmental variables in the CCA.

4.2.2 Canonical Correspondance Analysis

This technique, a multivariate direct gradient analysis method, allows variation in species and species abundance, in this case between quadrats, to be directly related to environmental gradients. Data from all quadrats and eleven environmental variables were initially included. These included the seven variables discussed in section 4.1, distance and the three DCA axes.

Table 4.3 gives eigenvalues and the percentage of total variation in the data set accounted for, by each of the four principal axes. As before, the eigenvalues indicate by their size, the relative importance of each of the four axes in describing the variation between samples. From these values it would seem that there is little difference in the importance of the four although, as always, the first describes most variation. The percentage values when summed come to substantially less than 100% indicating that environmental variables other than those explored here are causing a substantial quantity of the variation in the data set.

Table 4.4 shows canonical coefficients and corresponding t-values for each of the environmental variables on each of the four axes. These figures give an indication of the importance of each environmental variable in explaining the sample variation described by each axis. Strictly speaking these t-values can not be used to test whether the affect of each environmental variable on the data set is significant or not, because they are based on canonical coefficients. They may still give a good indication however as to relative importance and likely significance of each variable.

Table 4.3 Eigenvalues of the first four principal axes of the CCA, plus values for 'percentage Variation accounted for' by each CCA axis.

Axis	Eigenvalue	Percentage Variance
1	0.295	20.2
2	0.239	16.4
3	0.223	15.3
4	0.142	9.7

From table 4.4 we can see that on the first principal axis the two environmental variables most responsible for separation of the samples are soil temperature in a negative direction and the DCA axis 2 in a positive direction. Separation on the second principal axis is strongly effected by soil temperature, illumination and DCA axis two in a positive direction and PAR, organic content and air temperature in a negative direction. Distance contributes strongly to sample separation along axis three.

Significance of the relationship between the environmental variables as a whole and the sample variation described by both the first axis and all axes was tested using the Monte-Carlo permutation test. With 99 permutations performed, environmental variables were found to be significantly related to sample variation on the 1st canonical axis (P = 0.02), and on all axes (P = 0.01).

Figure 4.5 shows the constrained ordination diagram of variation in sample data plus environmental biplots for CCA axis one and two (biplot scores are multiplied by ten to emphasise the direction of their ~~a~~effect). It is immediately clear that the principal environmental variables affecting ordination on these two axis together, are temperature and light variables in one direction and moisture and organic content in the other.

Table 4.4 Canonical coefficients and T-Values of Environmental Variables Measured by each CCA axis.

	Axis 1		**Axis 2**		**Axis 3**		**Axis 4**	
	Ca Coeff	T-value	Ca Coeff	T-value	Ca Coeff	T-value	Ca Coeff	T-value
distance	0.053	0.63	-0.196	-2.27	0.419	9.18	-0.020	-0.36
pH	-0.129	-1.85	-0.121	-1.68	-0.044	-1.15	0.008	0.18
org con.	-0.022	-0.30	-0.233	-3.00	-0.130	-3.17	-0.181	-3.61
moist con.	-0.073	-0.91	0.040	0.48	0.036	0.82	0.191	3.58
air temp	0.103	0.98	-0.307	-2.83	0.037	0.64	-0.245	-3.51
soil temp	-0.288	-3.25	0.496	5.40	-0.086	-1.78	0.026	0.44
Illumin	-0.050	-0.3	0.410	2.35	0.298	3.24	-0.538	-4.79
P.A.R.	0.050	0.3	-0.319	-1.84	-0.171	-1.87	0.598	5.37
DCA Ax.1	-0.066	-094	0.001	0.02	0.182	4.7	-0.120	-2.54
DCA Ax.2	.582	8.57	0.344	4.89	-0.073	-1.96	-0.058	-1.29
DCA Ax.3	0.016	0.26	0.054	0.83	0.003	0.08	-0.072	-1.73

Effectively those samples/quadrats drawn upwards, towards the temperature and light variables, are those which contain species and combinations of species for which these resources are particularly important. The further towards the arrow heads the samples are drawn the more important these resources are to the species within them. Within the group of samples drawn out in this direction are nine of the ten quadrats which lie along the edge of the wood. Of the remaining twelve a further five are from the 5 metre transect. It is clear that transects at or near the edge of the woodland contain relatively more species for which warmth and light are important. The species associated with these quadrats are many, although few are exclusive to the edge environment as a few unusual interior quadrats are also found in this group and support similar ground floral communities. Figure 4.6 shows the ordination diagram of species scores with environmental biplots (biplot scores are multiplied by one hundred to emphasise the direction of the effect), species codes can be found in appendix 8. Those species which are found to be affected most by light and temperature variables and are therefore found more frequently in the three transects closest to the edge include *Veronica montana, Stellaria media, Anthriscus sylvestris, Lamium album, Bromus ramosus, Deschampsia cespitosa, Geum urbanum, Rumex sanguineus and Cerastium fontanum.* Slightly further removed from the arrowheads are species such as *Geranium robertianum, Stellaria graminea, Galium aparine and Heracleum sphondylium.*

In the opposite direction, samples/quadrats which contain species to which the environmental characteristics of moist organic soils are important, are drawn out. Of the 21 samples found in this group only one is from the 0 and 5 metre transects indicating that quadrats in the interior of the woodland contain relatively more species of this type. From figure 4.6 we can see that those species found to occur more often in these conditions include *Oxalis acetosella, Lonicera pericylmenum, Holcus mollis, Deschampsia flexuosa, Dryopteris dilatata, Dryopteris carthusiana* and *Lolium perenne.*

Although it is clear that DCA axis two has a strong effect in the positive direction of the 1st principal axis, it can be seen that this affects very few of the samples. It may be an indication however that ground flora in certain quadrats is affected by a particular and unusual type of canopy, pH and the other DCA axes do not appear to account for any significant quantity of the variation in the data set.

Axes three and four of the CCA analysis provided little improvement on the description of the data set gained in axes one and two. Samples are still drawn in different directions towards the two major groups of variables and although some further separation was gained, it provided no greater insight into possible causal factors.

Figure 4.5 CCA Ordination Diagram

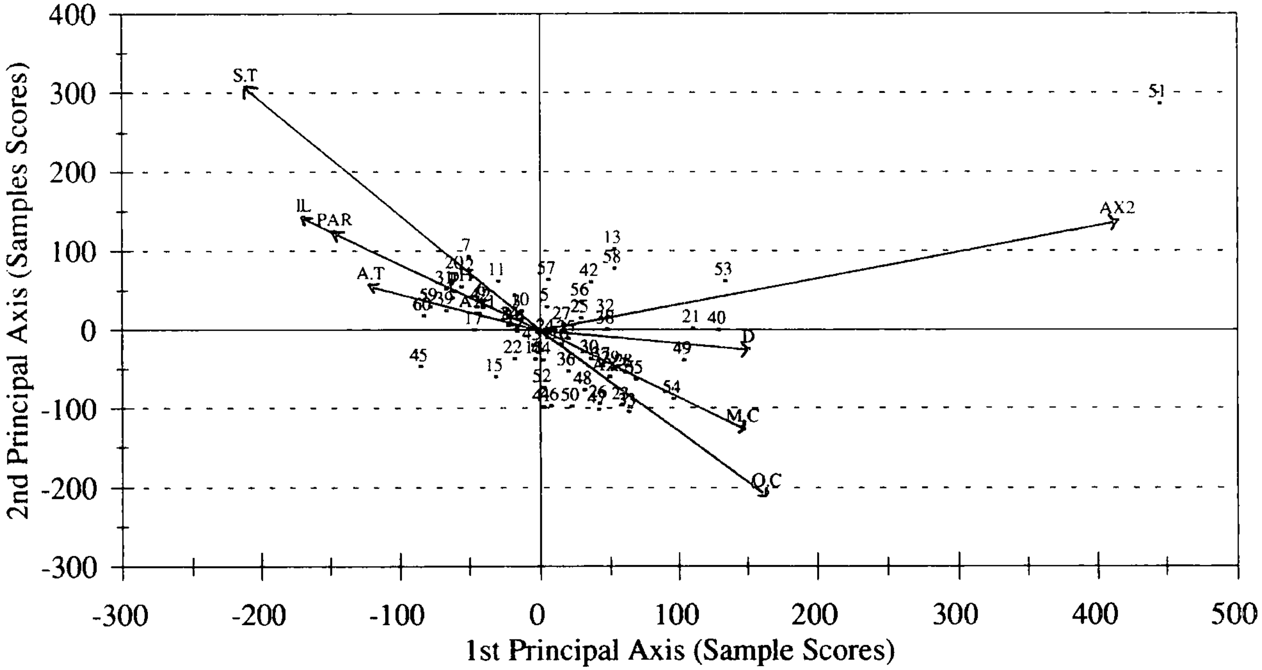
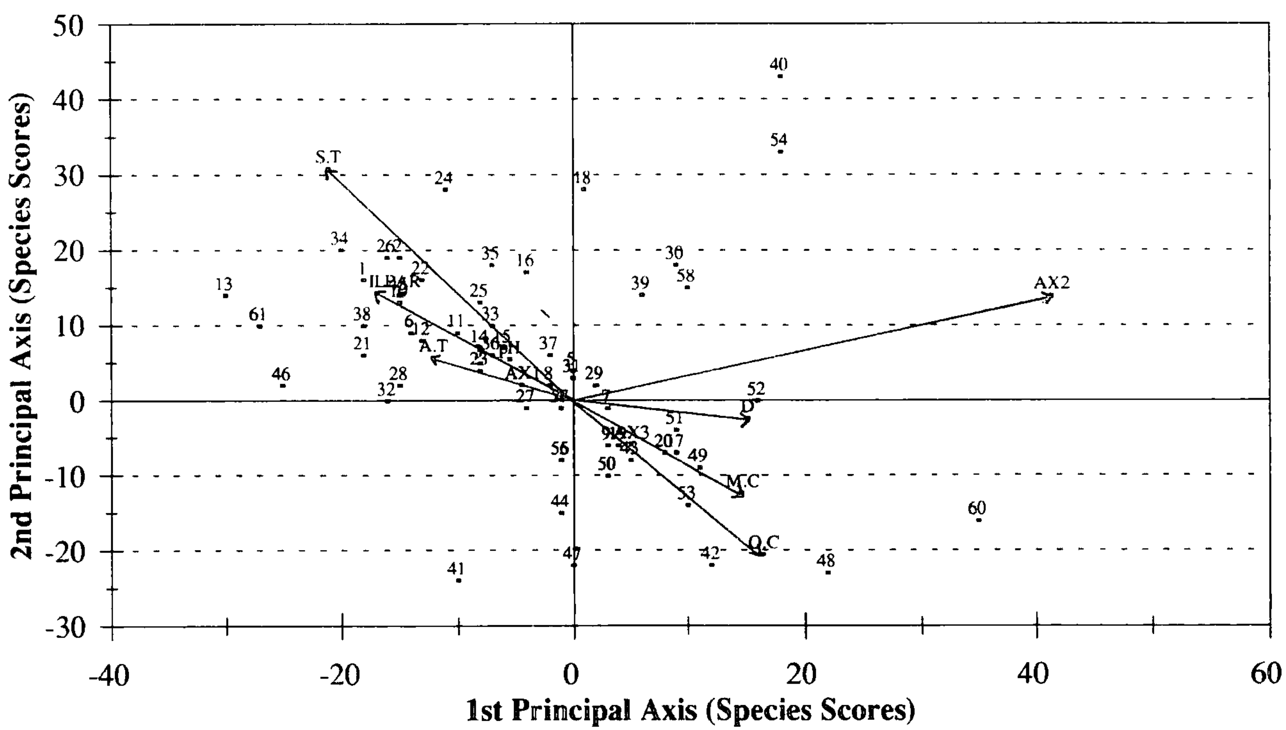


Figure 4.6 CCA Ordination Diagram



It is important to note at this point that for some species presence in, for example, edge quadrats may be due to an association with another species as opposed to a direct preference for edge microclimate. A ranked correlation table was produced using the Domin scores of all species in each quadrat, in order to consider this possibility. Table 4.~~8~~5 contains those species which had a correlation greater than 0.6, this must be considered in the interpretation of these results (for complete correlation table see appendix 8). It is also important to consider the possibility that variation which appears to be accounted for in the way described above, may actually result from unmeasured environmental variables which happen to correspond, in their pattern of variation, with measured variables.

Table 4.5 Species with correlation coefficients of greater than 0.6. (s = seedling)

Correlated Species	Correlation Coefficient
Quercus petraea (s) - *Sambucus nigra* (s)	0.7
Dactylus glomerata - *Urtica dioica*	0.65
Stachys sylvatica - *Chrysosplenium opp.*	0.7
Carpinus betulus (s) - *Sambucus nigra* (s)	0.7
Urtica dioica - *Chrysosplenium opp.*	0.64
Viola riviniana - *Valeriana officinalis*	0.96
Geranium sylvaticum - *Viola riviniana*	1.0
Geranium sylvaticum - *V. officinalis*	0.97

4.3 The ~~A~~Effects of Edge and Edge Related Environmental Variables on Vegetation Structure.

As herb growth performance has often been associated with environmental gradients (Matlack 1994), vegetation structure may also change with distance from the edge of the woodland. This hypothesis was tested with the use of classical statistics including Chi-square and two way analysis of variance.

4.3.1. Chi-square analysis Using Distance.

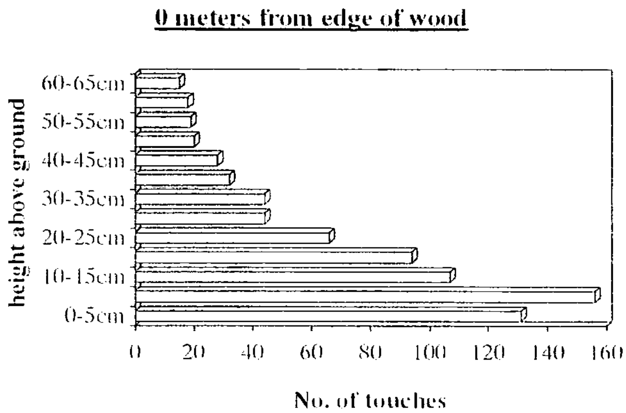
Chi-square tests were carried out for total vegetation and several individual species. Cumulative numbers of touches within each transect were used to establish if there was a significant difference in the numbers of touches of vegetation in each height category with distance into the woodland. Clearly this did not allow for any problems of heterogeneity within transects, however no practical way round this problem could be obtained. As later two-way ANOVA analyses revealed no significant heterogeneity of mean vegetation heights within transects, it was assumed that this was not a major difficulty.

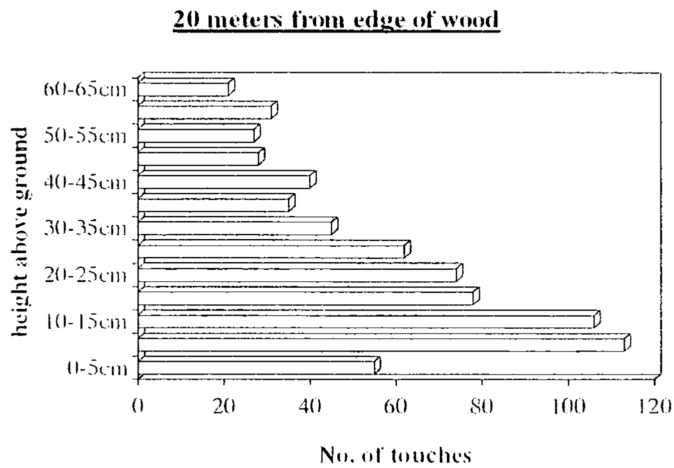
Table 4.6 gives the Chi-square values and statistical probabilities for numbers of touches of total vegetation, *Rubus fruticosus* and *Milium effusum* at all height categories and indicates whether there is a statistically significant variation within each height category between the different transects. In *Rubus fruticosus* and *Milium effusum* tests some height categories had to be combined due to low touch scores. Chi-square tests on many other species also encountered this problem and are not reported here due to the resultant instability of the results. Most of these species, as shown in section 4.2 are not actually present in all areas of the study site.

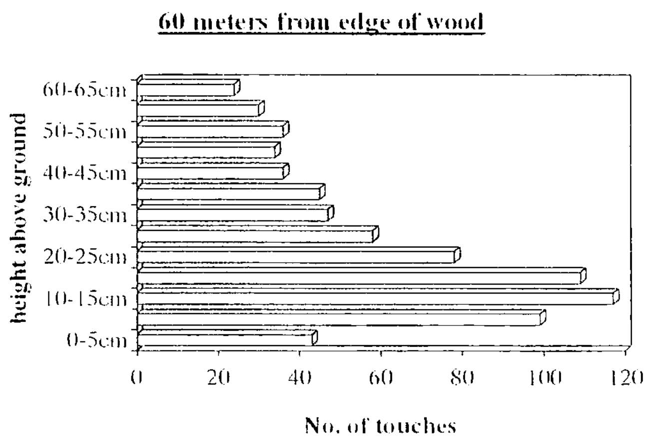
As can be seen from table 4.6 both total vegetation and *Rubus fruticosus* show significant variation between transects in both the lowest and the highest height categories. Interpretation of these values is possible with closer inspection of the original tables of observed and expected values which can be found in appendix 6.

For total vegetation, the highly significant results in height categories 0-5 & 5-10 cm are explained by 1. a greater number of touches in these categories than ex ? inspected, in the first two transects i.e. between 0 & 10 m into the woodland and 2. a smaller number of touches in these categories than expected, in the last three transects i.e. 20 - 60 m into the woodland. The opposite of this pattern explains the highly significant Chi-square values for total vegetation in height categories between 35 & 65 cm, i.e. a smaller number of touches from tall

Figure 4.7 Variation of total vegetation touches in all height categories at 0, 20 and 60 meters into the woodland.







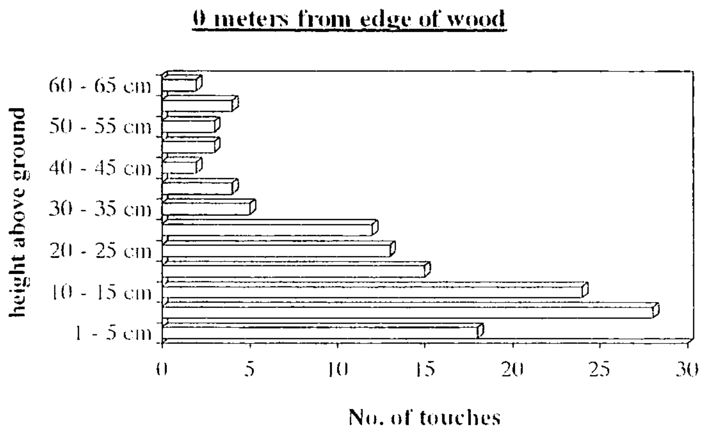
vegetation than expected towards the edge of the wood and a greater number of touches towards the interior. Intermediate height categories demonstrate no significant deviation from expected values at any distance from the edge of the woodland. Figure 4.7 illustrates this general trend of more abundant, short vegetation at the woodland edge and more abundant tall vegetation in the interior.

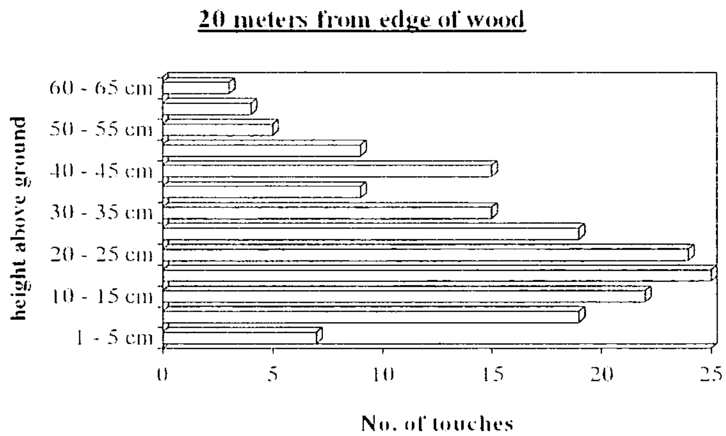
The results for the same analysis of *Rubus fruticosus* structure indicated an almost identical pattern. Bramble in the lower height categories was again found to be more frequent than expected at the edge of the woodland and less frequent than expected in the interior. In the upper categories although data for the range 50 - 65 cm had to be clumped to allow the analysis, Bramble touches recorded within the range 40 - 65 cm were similarly found to be more frequent in the interior than expected. Fig 4.8 illustrates this pattern.

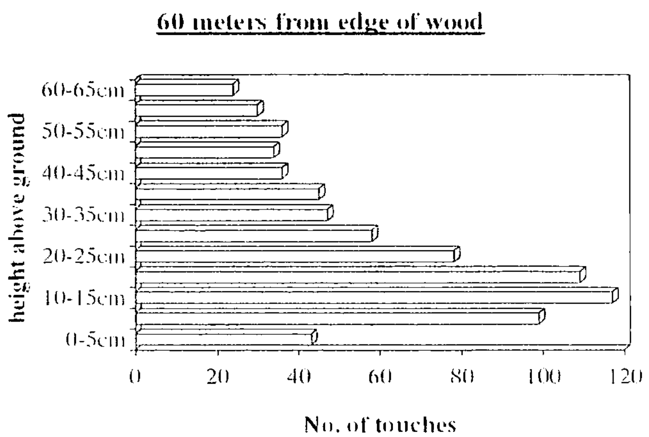
Table 4.6 Chi-square and P-values illustrating any significant variation within each vegetation height category with distance into the wood.

	Total Vegetation		***Rubus fruticosus***		***Milium effusum***	
	Chi² value	**P-value**	**Chi² value**	**P-value**	**Chi² value**	**P-value**
0-5 cm	63.14	0.01	35.95	0.01	30.07	0.01
5-10 cm	25.75	0.01	21.33	0.01	6.38	not sig.
10-15 cm	3.15	not sig.	11.16	0.05	12.39	0.05
15-20 cm	8.99	not sig.	12.00	0.05	8.19	not sig.
20-25 cm	9.42	not sig.	6.89	not sig.	7.76	not sig.
25-30 cm	7.44	not sig.	4.14	not sig.	10.49	not sig.
30-35 cm	0.56	not sig.	9.43	not sig.		
35-40 cm	18.69	0.01	10.43	not sig.	10.52	not sig.
40-45 cm	30.83	0.01	39.38	0.01		
45-50 cm	28.63	0.01	12.65	0.05		
50-55 cm	32.72	0.01			11.63	0.05
55-60 cm	32.21	0.01	59.44	0.01		
60-65 cm	25.80	0.01			-	-

Figure 4.8 Variation of *Rubus fruticosus* touches in all height categories at 0, 20 and 60 meters into the woodland







The only other Chi-square test which was successfully completed was that for *Milium effusum*. The pattern illustrated by this analysis is much weaker, probably due to the much smaller data set. It is still true to say however that for those categories which do exhibit a significant deviation from the expected values, the causal pattern is again the same as for total vegetation and Bramble.

4.3.2. Two way analysis of variance.

Two-way ANOVA analyses also indicated a significant change in the mean height of total vegetation and *Rubus fruticosus* with distance from the edge of the wood. In these analyses mean values from each individual quadrat were used so that the potential problem of heterogeneity within transects could be discounted. Table 4.7 shows the results of two-way ANOVA tests for total vegetation, *Rubus fruticosus* and *Milium effusum*. Inspection of the P-values indicates that there is a significant difference in mean height of total vegetation and *Rubus fruticosus* between transects although *Milium effusum* shows no such pattern. There are no significant difference values for quadrats within transects. Two-way ANOVA analyses on other individual species were not conducted due to the paucity of quadrats in which most of them occurred.

Table 4.7 Two-way ANOVA results illustrating significant variation in Mean Height of vegetation with distance into the wood.

	degrees of freedom	F value	P value
Total Vegetation	5 and ?	2.87	0.037
Rubus fruticosus	5 and ?	4.57	0.002
Milleum effusum	5 and ?	1.17	0.36

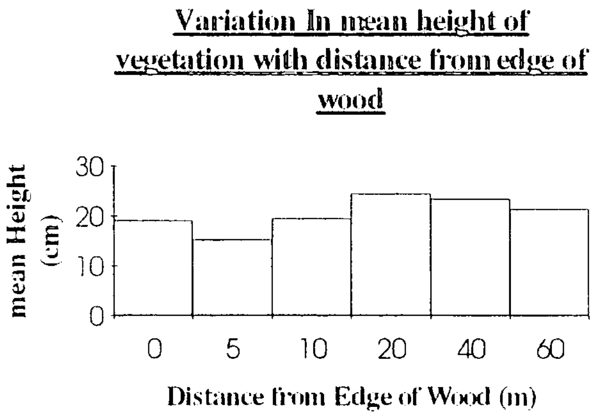
Having established the lack of significant variation within transects, figure 4.9 uses the mean height of vegetation for each transect to illustrate the direction of variation in mean height with distance into the woodland. For *Rubus fruticosus* in particular a clear trend towards increasing mean height with distance into the wood can be seen. A bar chart for *Milium effusum* is also included despite the insignificance of the two-way ANOVA results. It too would seem to indicate a general trend for increasing vegetation height from the edge to the interior of the woodland.

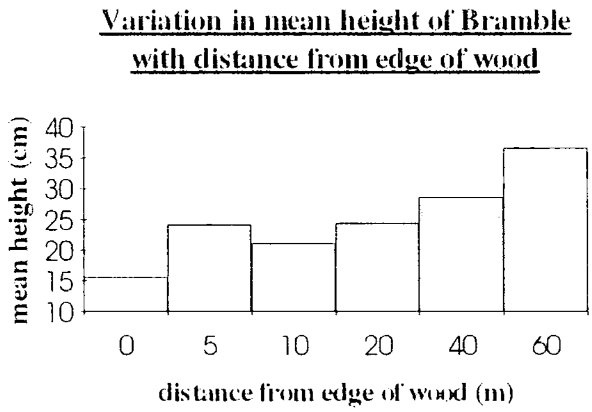
Having established that a pattern of variation in vegetation structure does exist with distance from the edge of the wood. Further Chi-square tests were conducted, this time testing variation in vegetation structure with changes in environmental conditions. The aim of this was to try to establish which environmental variables, known to vary with distance from the edge of the wood, were responsible for the changes in structure. Numbers of touches in each height category were compared for each environmental variable, having first divided each variable itself into between three and five categories.

Table 4.8 P-values indicating the significance of variation in numbers of total vegetation touches in each height category, with variation in each of six environmental variables

	Illumin.	P.A.R.	Soil Temp.	Air Temp.	Org. con.	Moist. con.
0-5 cm	0.01	0.05	0.01	0.01	0.01	0.01
5-10 cm	not sig.	not sig.	0.01	not sig.	0.01	not sig.
10-15 cm	0.05	not sig.	not sig.	not sig.	0.01	not sig.
15-20 cm	not sig.	0.05	not sig.	not sig.	0.01	not sig.
20-25 cm	0.01	0.01	not sig.	0.05	0.01	0.01
25-30 cm	0.01	0.05	0.05	not sig.	not sig.	not sig.
30-35 cm	0.01	not sig.	not sig.	not sig.	not sig.	not sig.
35-40 cm	0.01	0.01	not sig.	not sig.	not sig.	not sig.
40-45 cm	not sig.	not sig.	not sig.	not sig.	not sig.	not sig.
45-50 cm	not sig.	not sig.	0.01	0.05	0.01	not sig.
50-55 cm	not sig.	not sig.	not sig.	0.05	0.05	not sig.
55-60 cm	not sig.	not sig.	not sig.	not sig.	0.01	not sig.
60-65 cm	not sig.	0.05	not sig.	not sig.	0.05	not sig.

Figure 4.9 Variation in Mean Height of Total Vegetation, *Rubus fruticosus* and *Milium effusum* with distance from the edge of the wood.





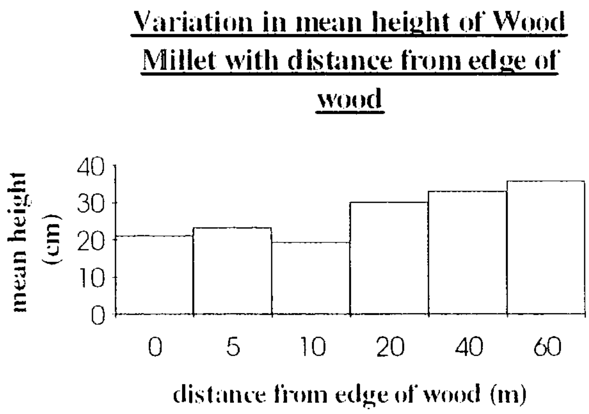


Table 4.8 shows the Chi-square values and their significance for all height categories in each of the six analyses completed. These analyses were only completed for total vegetation as it was felt that this would be most likely to reveal any significant patterns. Also only those variables previously demonstrated to have a strong correlation with distance and an ~~affect~~ effect on the vegetation were analysed.

As is evident from table 4.8 most environmental variables do not appear to affect vegetation structure in the way we would expect if they alone were responsible for the pattern found in Chi-square tests conducted using distance. Soil and air temperature and illumination and P.A.R. have all been shown to decrease sharply with distance from the woodland edge. If these represented the important influences on vegetation structure we would expect to see a pattern of more frequent short vegetation than expected in high light and temperature quadrats and more frequent tall vegetation than expected in lower light and temperature quadrats. This is obviously not the case and in fact there is no clear pattern of significance for any of these variables over the range of vegetation heights. Indeed it would have been surprising had such patterns emerged as they would have suggested that higher light and temperature levels resulted in (less etiolation?) decreased growth. Soil organic and moisture content on the other hand have been shown to increase with distance from the edge of the woodland and could logically account for some of the structural changes found. No clear pattern exists in the Chi-square results for soil moisture (for observed and expected tables see appendix 6), however inspection of the organic content data indicates that patterns of structural variation with increasing organic content are very similar to those seen for increases in distance from the edge of the wood. This introduces the idea that edge orientated changes in organic content maybe one of the important factors regulating overall community height however, as for vegetational composition, it is very likely that other variables, not investigated here are equally important.

5.0 Discussion

5.1 Microclimatic changes at the edge of the woodland

The results of this study have demonstrated clear and specific alterations in several microclimatic elements at the boundary of this woodland. Many of the findings coincide with previous work, conducted in both temperate and tropical areas and suggest the existence of a 'transition zone' where important environmental variables are subject to the 'edge effect'. The boundary of a woodland separates the wide climatic fluctuations of surrounding open habitats from the relatively stable environment of the woodland interior. It is crossed by gradients of light, temperature, moisture etc. which have often been implicated in the performance of forest herbs (Matlack 1994). In this study significant gradients in six such microclimatic and edaphic factors have been exposed.

At the northerly edge of Moorhouse wood, illumination, P.A.R., air temperature and soil temperature were all shown to be significantly greater than in the interior. Illumination and P.A.R. decreased rapidly over a 5-10 metre distance and continued to decline more gradually further into the wood. Similarly soil and air temperatures fell sharply from the edge of the woodland to the interior whilst soil moisture and organic content underwent a slight but significant increase in this direction. It would appear that a microclimatic transition zone approximately 10 metres wide is in place at the northern boundary of Moorhouse Wood.

These results are mostly as predicted and compare favourably with previous studies both of woodland edges and of woodland gaps. Gap dynamics have been widely studied and although the changes in microclimatic conditions within a gap are usually weaker than at an edge, there are many similarities. As reported earlier, studies conducted by Laurance (1991) and Williams-Linera (1990) at tropical forest margins, illustrated very similar responses to fragmentation as those described in this study. Increases in air temperature and solar radiation, and decreases in soil moisture were all apparent at the forest edge

(Laurance 1991). An air temperature transition zone between 2.5 and 12 metres into the forest was recorded and overall, environmental conditions were said to be significantly ~~e~~affected up to 20 metres into the woodland (Williams-Linera 1990). Collins and Pickett (1987) reported increased radiation levels reaching the herb layer in gaps in a northern hemisphere hardwood forests and a variety of other authors (Matlack 1993, Runkle 1987, Moore and Vankat 1987) have described edge and gap effects in light, temperature and moisture variables.

At an artificial edge, where solar radiation enters the trunk space, the woodland floor may become a thermodynamically active surface (Matlack 1993). The increased radiation load will naturally result in the higher illumination and temperature levels frequently reported. In this study however, decreased soil moisture levels were also recorded; this disagrees to a large extent with many past studies (e.g. Williams-Linera 1990). Collins and Pickett (1987) reported that soil moisture levels on the edge of a woodland will often increase due to a greater amount of precipitation reaching the woodland floor. Soil moisture depends on precipitation throughfall, evaporation and transpiration. A canopy intercepts more rainfall and returns a large proportion to the atmosphere without it ever reaching the ground. The apparent discrepancy between this and other reports may be due to a number of factors but is most likely to be explained by; 1. In the present study, canopy density does not increase as expected with distance from the woodland edge. As a result there is no reason to expect more rainfall to reach the soil at the boundary. 2. soil moisture measurements were taken from the top 10cm of the soil. As other authors have described, moisture in the top few centimetres is often decreased at the edge of a woodland due to increased evaporation, particularly during the summer months (Laurance 1991, Auclair 1975). The results presented here may simply not reflect the prevailing soil moisture conditions throughout the year or at a greater depth.

Very few studies have included measurements of soil organic content in their description of the woodland boundary. The fact that this variable seems to run parallel with soil moisture levels however, is not surprising. Cool damp conditions often hinder the process of complete decomposition of plant material and we would therefore expect to encounter higher levels of organic matter in the moist soil of the woodland interior.

Within this study three environmental variables did not show a significant edge orientation. The fact that this is an area of secondary woodland and is a highly and continually disturbed habitat probably explains why no clear patterns of canopy density and basal area, with distance from the edge of the wood, were found. The lack of any pattern of variation in pH is a little harder to explain but probably reflects the large number of factors which can influence this variable e.g. underlying parent material, historical influences etc.

One thing which is clear from both this and previous work in this area is that very few generalisations can be made. Each microclimatic element responds differently to the creation of an artificial edge and responses can vary widely between different sites. Matlack (1993) recorded elevated light zones extending 35m into wooded sites but conceded that even within this one study of temperate deciduous forests, there was considerable site-to-site variation in the strength and character of edge effects. Other studies have reported edge effects reaching only 10m into wooded areas (Wales 1972), whilst some have found effects at more than 50m into a woodland. The magnitude of alteration of the environment due to edge creation depends on many things e.g. shape, size, age, aspect, time of year, canopy density etc. (Collins and Pickett1987). South facing edges in the northern hemisphere are exposed to a great deal more direct beam radiation than north facing edges and as a result tend to show much greater edge effects and wider microclimatic transition zones (Matlack 1994). The fact that this study was conducted on a north facing edge however, indicates that the consequences of fragmentation, whilst possibly weaker on a north facing edge, may still be considerable. Age of the woodland is also an important consideration as regrowth at the woodland boundary will ameliorate the climatic influence of variable seems to run parallel with soil moisture levels however, is not surprising. Cool damp conditions often hinder the process of complete decomposition of plant material and we would therefore expect to encounter higher levels of organic matter in the moist soil of the woodland interior.

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The strength of microclimatic responses at a woodland edge and the resultant width of transition zone will have important affects on the woodland ground floral community and therefore the ability of an area to sustain a representative biota. It is important to remember though that the conditions reported here refer only to the summer months. During the winter the conditions on a north facing edge may be influenced by strong prevailing winds causing large drops in temperature and increases in soil moisture, even in the top 10 cm (Laurance 1991). Conditions during the spring and summer months are those most likely to affect the important growth and reproductive stages of herbaceous plants; conditions at other times however, may also play an important role in the distribution of woodland herbs. Many other aspects of the microclimate, not explored here, may also have an influence. For example it has been reported that light reaching the herbaceous layer in forest gaps is enriched in far red, green and blue light (Collins, Dunne and Pickett 1985). Consequences of edge formation such as these are also bound to influence the distribution of woodland herbs.

5.2 Affects of edge and edge oriented environmental variables on plant community composition.

Composition of the ground floral community at the northern boundary of Moorhouse Wood was demonstrated to be significantly ~~e~~affected by environmental conditions imposed by the 'edge effect'. Multivariate analysis techniques allowed the description of the variation in community composition with distance into the wood and demonstrated how this was related to microclimatic and edaphic variables.

It was not the intention of this study to look at canopy composition except in relation to its ~~a~~effect on the ground flora. The DCA was undertaken simply to highlight any canopy patterns which might be relevant to the distribution of the ground floral species. In the process however, a picture of how canopy composition itself varied with distance from the edge of the wood was constructed and requires some discussion.

5.2.1 Variation in canopy composition with distance from the edge of the wood

Results of the DCA appear to suggest that many traditional deciduous woodland species are unable to regenerate at the boundary of a fragmented woodland. There has been ample time since the creation of this edge for the establishment of new individuals of many species e.g. *S. aucuparia, F. sylvatica, C. betulus*, and yet there is no evidence whatsoever that these species are recolonising this boundary. There are several possible explanations for this;

1. Disturbance levels at the edge of the woodland are too great to allow establishment.

2. Environmental conditions at the edge are no longer suitable for the success of these species.

3. They are out-competed by species which are better adapted for 'life on the edge'. It is most likely that a combination of these factors has resulted in the absence of many species from the woodland boundary. Some evidence of this can be obtained by studying the ecology of those species which dominate at the edge and those which seem to be excluded.

Two of the dominant species in edge transects in this study were *A. pseudoplatanus* and *C. monogyna*. Both of these possess characteristics which would suit them to the edge environment. In Grime, Hodgson and Hunt (1988) *A. pseudoplatanus* is described as a common seedling weed which establishes easily in unshaded conditions. The seedlings are capable of more rapid growth than most British tree species and it is reported that they are usually the first to colonise highly disturbed sites. *C. monogyna* is also reported to be highly tolerant of disturbance, occurring frequently in heavily grazed habitats. Some of the

C. monogyna on the edge of this site may have been planted but this would only account for a small proportion. The species is described as frequent in unshaded positions and seems to have difficulty regenerating in shaded conditions.

Species which do not occur on the edge of this woodland include *S. aucuparia, F. excelsior, B. pendula* and *F. sylvatica*. In wooded habitats *S. aucuparia* is reported as always forming part of the wood itself rather than the scrub and requiring shaded conditions for establishment and seedling growth (Grime, Hodgson and Hunt 1988). The small seedling is considered to be exceptionally shade tolerant (Pigott 1983). *F. sylvatica* also exhibits ecological preferences which seem to make in unsuited to the edge environment. It requires moist conditions for establishment and once again seedlings are highly shade tolerant (Watt 1934).

The position is not quite as clear however as the story so far would suggest. Many species which occur only in the interior such as *B. pendula and F. excelsior* should, theoretically, be able to colonise the unshaded conditions of the edge. *F. excelsior* is said to prefer sheltered and moist soils but it also thrives in fairly open conditions (Grime, Hodgson and Hunt 1988). It is likely, in this case, that levels of disturbance and exposure place the woodland edge in the extremities of the ecological niche of this species, allowing it to be out-competed by the more vigorous *A. pseudoplatanus* and *C. monogyna*. Equally *B. pendula* is said to be unable to persist under shaded conditions (Grime, Hodgson and Hunt 1988). Although this may well be the case it would seem that canopy disturbance, away from the woodland edge, is sufficient in this case to allow its continued presence. The presence of large numbers of *Q. petraea* at the edge of the woodland would also seem strange. The ecological preferences of this species would not seem to suit it to the edge environment however this may simply be explained by the dominance of *Q. petraea* throughout the woodland and the possibility that edge individuals of this long lived species are those which have survived from before edge creation.

5.2.2 The ~~a~~effects of edge related environmental variables on ground floral community composition.

Previous studies which have considered the ~~a~~effects of edge creation on the herbaceous community of woodlands have all found considerable alterations, believed to be due to environmental change. This basic 'truth' is no longer in question. However, as with microclimatic elements themselves, site-to-site variation causes disagreement about the details of edge ground floral community alterations. The results presented here suggest a number of things about the situation on the northern edge of this particular woodland and in general these agree with many previous reports. In this study it has been shown that;

1. close to the boundary of Moorhouse Wood, many species with ecological preferences which suit them to the edge environment, are increased in abundance.
2. that species which are not well adapted to edge conditions are, on many occasions, restricted to the woodland interior.
3. that most species present on the woodland edge are also found in the interior but a few non-woodland species are exclusively edge dwelling.

Although most studies admit to some alteration of the herbaceous community at a woodland edge, most disagree about the strength of the effect. Laurance (1991) reported an elevated abundance of 'light loving' species at the edge of a wooded area but, as mentioned earlier, Williams-Linera recorded no significant changes in floristic composition from the edge to the interior. Despite clear microclimatic alterations and abundant light-loving species in adjoining habitats, in the Williams-Linera study, light demanding species were not more abundant at the forest edge. Williams-Linera does comment that changes in floristic composition at the edge of a temperate deciduous woodland may be more pronounced than in the tropics. Changes in the composition of herbaceous communities, correlated with edaphic and microclimatic variation, have been established in a wide variety of temperate studies (Matlack 1994, Pitelka, Stanton and Peckham 1980, Wales 1972) but results are still equivocal.

The results of the present study show that, in this case, there is a division of species into those which are most abundant in edge transects and appear to have requirements for warm unshaded conditions and those which are not abundant at the woodland edge and which would appear to require moist organic soils. Once again the recognised ecological preferences of these species may indicate whether this is actually the case. Most of the species which are abundant on the edge of the woodland are true woodland species but ones which would normally only dominate in natural gaps or in disturbed areas. Most are also flexible enough to have become colonisers of other habitats. *Veronica montana* for example, is described as usually becoming dominant where other species have been suppressed by disturbance. *Stellaria media* is a short lived ruderal which has a rapid growth rate and is usually associated with recently disturbed soils (Grime, Hodgson and Hunt 1988). Others such as *Bromus ramosus* and *Cerastium fontanum* are known to prefer drier unshaded sites and *Geum urbanum* will only set seed in unshaded conditions (Grime, Hodgson and Hunt 1988).

In the woodland interior there are many species which are simply not found at the woodland edge. The reasons for this are likely to be similar to those which prevented the recolonisation of the woodland boundary by many tree species. *Oxalis acetosella* is a small prostrate species with a slow growth rate and high shade tolerance. It is physiologically attuned to low light and temperature conditions and, due to its shallow root system, is restricted to areas with continually moist soils (Grime, Hodgson and Hunt 1988). *Dryopteris dilatata* is long lived, highly shade tolerant and also has a requirement for continually moist conditions. Other species such as *Lonicera periclymenum* and *Deschampsia flexuosa* are relatively slow growing, shade tolerant species and are also restricted to the woodland interior. Once again some species which only occur in the woodland interior should, theoretically, be able to colonise the edge. *Holcus mollis* is a woodland species which prefers reasonably open conditions but seems to be excluded from the boundary area either due to competition and disturbance or to some factor which has not been explored in this study.

As the results of the CCA demonstrated, a significant amount of the variation in the herbaceous community composition was not explained by the environmental variables investigated in this study. Many other factors may influence the distribution of species in this woodland including soil depth, nutrient content, historical disturbance, winter chilling etc. Species interactions and associations are also likely to play an important role in community composition at any one point and are outside of the scope of this study.

One major area of discourse in previous studies of this subject has always been whether edge conditions, created by fragmentation of a habitat, allow the invasion of non-woodland species from surrounding man-modified habitats, into the woodland ecosystem. Laurance (1991) reported that fragments of Costa Rican forests were subject to 'massive seed rain' from generalist plants in adjacent habitats which are gradually altering the composition of the original forest. This finding has been substantiated by many studies (e.g. Matlack 1994, Collins and Pickett 1987, Janzen 1983); however others have disagreed and concluded that edges offered little opportunity for entry by invasives and ruderals (Williams-Linera 1990).

In this study it was established that whilst most species found at the woodland edge were also present in the interior, a few were not woodland species at all. *Anthriscus sylvestris* is a ruderal species, described as a 'follower of humans' (Grime, Hodgson and Hunt 1988), which is generally only found in hedgerows and on grasslands. This species was almost exclusive to the edge transect. Similarly *Lamium album* is a species which dominates where others have been suppressed by disturbance. It prefers light, well drained sites and is, again, characteristic of hedgerows and roadsides.

Although many studies have shown that non-woodland species can and sometimes do invade at the edge of a fragmented woodland, most also point out that it is rare to find these species colonising beyond the microclimatic transition zone (Laurance 1991). The current results agree with these conclusions and with the hypothesis that a microclimatic and vegetational transition zone may even act as a buffer against further change to the woodland interior. In this case however, the woodland area has been so fundamentally altered by disturbance that it is difficult to conclude that no non-woodland species have extended beyond the edge zone. Some may simply have colonised throughout the entire woodland.

In conclusion the results of this part of the study show that ground flora community composition is fundamentally altered by the gradients of microclimatic elements created at the boundary of the woodland. Although some non-woodland species have invaded and colonised at the edge, most alterations relate simply to changes in abundance of woodland species. These changes in dominance at the woodland edge are likely to have altered the community ecology of the area. Dominance of a particular species is, however, unlikely to lead to its dominance in the interior of the woodland where microclimatic conditions are not affected by proximity to the edge.

5.3 E~~A~~ffects of edge and edge oriented environmental variables on plant community structure.

Despite the fact that only the briefest of analyses were possible with the data set acquired from point quadrats, a very clear pattern of changes in vegetation structure, from the edge to the interior of the woodland, was immediately apparent. Effects such as these have been reported in past studies (Williams-Linera 1990). In this case however, as at no other time in these results, it was indicated that something other than the microclimate was the overriding factor in determining patterns of variation.

5.3.1 All ground floral vegetation.

Both chi-square and two-way ANOVA tests indicated a clear gradient in the height of ground floral vegetation with distance from the edge of the wood. Chi-square analyses demonstrated a higher than expected abundance of vegetation in the height bracket 0-10cm at the edge of the woodland and a higher than expected abundance of vegetation in the height bracket 35-65cm in the interior. In conjunction with an increasing mean vegetation height from the edge to the interior, (as indicated by the two-way ANOVA), it is clear than in general vegetation at the edge of this woodland is shorter than in the interior. There are two possible explanations for this; 1. that there is a greater abundance of smaller species at the edge of the woodland. 2. that individuals of all species at the edge of the woodland do not grow as tall as in the centre.

Both of these explanations are likely to contribute to the pattern seen, but to what extent does the edge microclimate plays a significant role in the production of these patterns?. A great deal of work has been conducted into the affects of microclimatic change on the performance of forest herbs. Most of the affects are well known and unsurprising. Although the environmental responses of woodland herbs will vary depending upon their physiology, high light and temperature conditions have frequently been linked to increases in assimilation rates, vegetative growth and reproductive potential (Moore and Vankat 1986, Collins, Dunne and Pickett 1985, Matlack 1994). Theoretically the high light and temperature conditions of the edge, if no other factors were involved, should lead to increases in vegetation height at the edge of the woodland; totally the reverse of what was actually found in this study.

Statistical investigation of structural responses to increases of temperature and light, at this woodland edge, indicate that in fact variation in these variables has little to do with the structural patterns seen and demonstrate that other factors are far more influential. Chi-square analyses revealed that the only environmental variable which was significantly linked to structural changes in the vegetation was soil organic content and suggest that the lower levels of organic content at the edge of the woodland may have a detrimental effect on vegetation growth.

Despite this, it is the conclusion of this study that edaphic and microclimatic variation has little influence in the structural differences at the edge of this woodland. It has been reported in some studies that increases in illumination and P.A.R. may actually have very little effect on the growth patterns of forest herbs, as many are already at their light saturation point in the shade of the woodland interior. These species would be unable to benefit from, and may even be detrimentally affected by, increases in these resources. The same may also be true of air and soil temperatures and may explain the apparent lack of vegetational response to these variables. It is also the conclusion of this study that changes in organic content into the woodland, although statistically significant, are unlikely to have any real ecological significance when considered independently of other variables. Similarly, although previous studies have suggested that soil moisture is an important factor in determining herb layer structure no evidence of such an effect was found here (Anderson, Loucks and Swain 1969).

Whether changes in vegetation structure at the edge of the woodland are due to stunted growth or to changes in species abundance, it is far more likely that high levels of disturbance, and not the edge microclimate itself, are responsible. Disturbance at the edge of the woodland could account for both a decrease in the height of individuals which were not well suited to these conditions and for an increase in the abundance of species which were more suited to this environment. High disturbance rates select for fast-growing, short-lived species which place a high priority on reproduction (Grime 1974). These species rarely grow to the size of longer lived perennial woodland herbs which are, to a large extent, excluded from the boundary area.

5.3.2 *Rubus fruticosus* and *Milium effusum*.

Identical patterns of structural change with distance from the edge of the wood were also illustrated for both *Rubus fruticosus* and *Milium effusum* (although for the latter, significance of the pattern was less clear). These results indicate quite clearly that decreases in vegetation height at the edge of the woodland are, at least in part, due to the presence of smaller individuals, and not just to changes in community composition favouring smaller species. *Rubus fruticosus* is said to achieve dominance more easily in shaded places (Watt 1934). *Milium effusum* is also described as a species which has improved vigour in moist, shaded places where the dominance of other species is suppressed. Overall it would seem that the woodland edge, far from providing an environment of improved conditions for growth, decreases the vigour of many species. Both microclimatic changes and increased disturbance levels at the woodland boundary ensure that many woodland species, which would otherwise thrive, are reduced in their potential for vegetative growth and may even be excluded completely.

One of the major points which has emerged from this study is the vast numbers of factors which may influence the way in which a woodland responds to the creation of an artificial edge. In this report only a few of the variables which may affect ground vegetation at the woodland edge were investigated and it has been shown that these do not account for a great deal of the variation found. It may never be possible to make generalisations about the affects of habitat fragmentation, but further study into a number of areas would build upon present understanding.

Within this study measurements of a number of other edaphic and microclimatic variables would have been useful. Nutrient (N and P) levels, soil depth, litter depth and soil coarseness may all have an influence on the vegetation as well as the quality, and not just the quantity, of light. Further studies would also be improved by the measurement of microclimatic variables at other times of the year and at edges with different ages and different aspects. One other aspect which, due to the lack of available time, was not considered in the interpretation of these results was the physiological plasticity of individual species and their ability to respond to edge microclimate changes. In depth studies of individual species are clearly vital for the complete understanding of ground floral distribution at the edge of a woodland.

In general, all plants use the same limited number of resources; growing space, sunlight, nutrients, oxygen, carbon dioxide and water. Plant performance varies in relation to composite environmental variables and depends upon underlying patterns of resource availability and conditions of temperature and atmospheric water potential. The central goal of plant ecology is to understand factors which control the distribution of plant species and therefore plant community composition (Barton 1993, Latham 1992). The creation of an artificial edge by fragmentation of a woodland habitat has been shown, here, to fundamentally alter the ground floral community by changing those patterns of resource availability. The creation of an edge affects every level of the plant community in a woodland. In the tropics, Laurance (1991) reported that exposure at the forest boundary led to a perpetual cycle of canopy damage. In other studies, previously discussed, invasion by non-woodland species has been reported and in many it has been suggested that this could lead to the gradual loss of native woodland species.

Understanding the extent to which isolated areas of woodland can sustain a representative biota gives an insight into the importance of preventing fragmentation and is essential when devising strategies of reserve design that will help to minimise the affects of habitat loss. It is possible that the creation of a vegetational transition zone at the edge of a woodland may offer some protection to the woodland interior should more serious threats to its integrity occur. Although it seems unlikely, it is also possible however, that this zone itself may become the more serious threat.

Summary

1. A microclimatic transition zone, approximately 10 metres wide, was found at the northern boundary of Moorhouse Wood. Illumination, P.A.R. soil and air temperatures decreased rapidly over this distance and continued to decline more gradually further into the wood. Soil moisture and organic matter content underwent a slight but significant increase in this direction.

2. Edge oriented patterns of variation were found in both canopy and ground floral community composition. In general, species with ecological preferences for disturbed or for warm and light conditions were increased in abundance at the edge of the woodland. Some evidence of invasion by non-woodland species was found but these did not appear to be colonising the woodland interior.

3. Ground vegetation structure was altered by proximity to the woodland edge. This was shown to be unrelated to most microclimatic variables and it is suggested that a high level of disturbance is more likely to be responsible for the decreased height of vegetation at the boundary.

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Appendix 1. Environmental Variable Scores for all Quadrats plus correlation Coefficients

quadrat	distance	pH	org. con. %	moist con %	air temp. °c	soil temp. °c	illum. (Lux)	P.A.R.	DCA axis1	DCA axis2	DCA axis3
1	0	6.5	13.03	21.04	20.9	15.66	53.07	143.13	-110	-27	-80
2	0	4.45	12.3	23	21.61	16.26	66.5	188.13	-109	-54	-73
3	0	4.75	21.29	20.41	21.02	15.52	58.5	179.38	-106	-13	82
4	0	4.75	17.1	26.52	21.39	15.44	87.19	211.88	-110	-77	44
5	0	4.7	12.47	23.22	21.21	15.12	49.88	125	-105	-6	-65
6	0	4.5	11.96	20.1	20.55	15.29	18.72	73.5	-110	-77	46
7	0	3.95	11.91	19.88	20.31	15.52	21.47	42.94	-110	-80	-55
8	0	4.5	12.43	33.23	20.69	14.6	36.88	91.34	-110	-67	-152
9	0	4.3	7.41	19.7	21.01	15.99	76.38	301.25	-112	-100	-161
10	0	4.3	10.94	29.1	20.32	14.34	38.02	96.5	-110	-71	-55
11	5	5	17.46	24.7	19.99	15.19	16	43.13	-106	-9	7
12	5	4.75	16.71	39	19.77	14.51	13.13	34.88	-109	-58	-1
13	5	4.2	16.98	36.41	19.52	14.45	11.7	31.25	16	121	51
14	5	4.25	28.66	41.82	19.84	14.59	10.01	27.69	-106	-13	85
15	5	4.45	24.58	62.48	20.27	14	11.24	25.44	-109	-63	-74
16	5	4.4	24.06	41.86	20.01	13.78	31.82	49	-106	-7	-56
17	5	4.7	22.77	32.23	20.54	15.19	12.7	32	-109	-61	73
18	5	4.95	27.96	31	20.3	14.43	40.19	112.69	-106	-13	82
19	5	4.75	12.18	24.93	20.49	14.54	29.07	87.69	-109	-66	1
20	5	6.3	14.12	36.39	20.32	14.99	94.38	223.13	-110	-27	-80
21	10	6.6	8.38	18.08	19.91	14.46	26.54	51.94	-121	-193	313
22	10	4.95	15.32	24.54	20.39	14.48	23.63	111.5	-113	-78	202
23	10	4.1	22.73	30.39	20.34	13.33	26.9	94.54	-106	-13	82
24	10	5.35	14.68	27.36	19.9	14.09	7.01	20.42	-105	-6	-65
25	10	4.2	18.11	33.25	20.41	14.54	14.95	22.51	-100	35	-167
26	10	4.05	29.06	29.3	20.38	13.73	14.28	34.13	-106	-9	9
27	10	4.45	16.95	28.2	20.06	14.21	18.5	48.82	-106	-12	83
28	10	4.15	15.69	34.1	19.74	12.88	7.13	19.82	-106	-13	85
29	10	3.95	18.72	42.52	19.63	12.91	6.92	17.09	-106	-15	92

30	20	4.2	19.62	41.7	19.97	13.43	24.76	51.54	-107	-18	161
31	20	4	23.76	37.9	18.85	14.21	8.06	13.07	799	-9	0
32	20	4.45	13.57	49.91	19.95	13.75	18.63	51.94	-95	45	111
33	20	4.1	22.43	41.31	19.91	12.77	13.32	34.77	-106	-9	9
34	20	4.4	17	27.65	19.8	14.11	5.88	12.5	696	14	0
35	20	4.4	14.06	25.38	19.69	13.79	4.75	19.24	-108	-38	105
36	20	4.3	16.2	36.76	19.57	13.19	12.4	36.88	-109	-57	-1
37	20	4.3	14.09	36.88	20.09	13.46	10.74	34.63	-106	-11	17
38	20	4.5	18.06	30.02	19.89	14.05	20.44	69.63	-96	44	46
39	20	4.3	14.18	19.77	19.11	14.24	14.83	44.5	148	-125	-28
40	20	5.2	11.76	23.99	19.47	14.77	9.27	30.88	-121	-223	-65
41	40	4.5	26.29	40.41	19.65	13.34	12.64	25.12	115	-41	9
42	40	4.9	19.94	31.19	19.51	14.73	8.69	19.82	-34	106	73
43	40	5.7	11.69	32.07	19.37	14.14	11.29	84.07	-105	-2	-137
44	40	5.7	10.16	38.71	20	13.94	5.99	20.16	-102	-16	-68
45	40	5.2	12.92	43.07	19.8	14.34	5.98	15.09	-115	-151	-184
46	40	4.45	21.9	49.14	19.87	13.26	12.12	35.44	-113	-77	267
47	40	4.1	27.51	51.49	19.85	13.14	21.32	55.38	-107	-17	159
48	40	4.2	25.29	43.22	20.03	13.68	17.5	47	-107	-16	158
49	40	4.3	23.68	34.94	19.75	13.65	6.68	38.19	29	145	-64
50	40	4.4	21.95	39.35	20.04	13.51	5.02	13.85	-112	-48	102
51	60	5.6	14.99	27.11	19.54	14.8	6.67	19	-154	905	-3
52	60	6.3	14.57	30.29	19.84	13.91	8.44	28	-106	-10	15
53	60	7.4	13.44	26.59	19.67	14.54	1.97	10.39	-124	329	15
54	60	5.65	23.8	40.16	19.66	13.16	21.12	63.7	21	141	-11
55	60	4.45	19.88	32.58	19.71	13.56	7.18	17.5	-95	48	-28
56	60	4.5	17.13	39.18	20.04	14.91	24.57	70.17	-70	67	73
57	60	4.25	14.6	32.13	19.5	14.95	12.32	32.38	-73	26	-1
58	60	4.35	11.9	54.89	19.59	14.36	27.13	74.32	-3	113	99
59	60	4.7	11.76	30.51	19.87	14.53	65.76	115.75	183	-132	5
60	60	4.1	10.91	28.08	20.19	15.16	35.75	89.13	189	-141	16

	Distance	**pH**	**Organic content**	**Moisture content**	**Air temp.**	**Soil Temp.**	**Illumin-ation**	**P.A.R.**	**DCA Axis 1**	**DCA Axis 2**	**DCA Axis 3**
Distance	1										
pH	0.194155	1									
Organic content	0.013221	-0.33361	1								
Moisture Content	0.293021	-0.26332	0.465922	1							
Air Temp.	-0.52821	-0.00504	-0.14927	-0.33233	1						
Soil Temp.	-0.28236	0.221069	-0.45181	-0.57489	0.553985	1					
Illumin-ation	-0.33278	0.100027	-0.24709	-0.2846	0.697162	0.559317	1				
P.A.R.	-0.34693	0.096012	-0.28912	-0.34895	0.707507	0.581136	0.936735	1			
DCA Axis 1	0.151941	-0.19989	0.096548	0.004975	-0.35769	-0.04103	-0.09802	-0.15132	1		
DCA Axis 2	0.378517	0.220843	0.105712	0.061863	-0.22439	-0.04258	-0.22747	-0.20601	-0.0455	1	
DCA Axis 3	0.099403	-0.08112	0.276549	0.149997	-0.15229	-0.30697	-0.16106	-0.18291	-0.05065	-0.01822	1

Appendix 2. Total tree density and basal area values for each quadrat

Tree Density (ha-¹)

quadrat		quadrat	
1	692.52	31	911.36
2	711.11	32	911.36
3	462.48	33	1129.86
4	1245.66	34	661.7
5	840.16	35	804.79
6	501.18	36	1007.81
7	946.98	37	4839.32
8	5173.47	38	2844.44
9	2138.4	39	591.27
10	1534.08	40	4596.38
11	653.27	41	1718.17
12	706.39	42	1083.85
13	1584.12	43	1189.06
14	1220.42	44	1616.12
15	613.44	45	1410.65
16	740.43	46	1057.57
17	1649.1	47	1264.2
18	1437.52	48	2138.39
19	997.12	49	2294.8
20	740.44	50	1334.4
21	1168.82	51	810.52
22	570.28	52	679.04
23	750.61	53	665.96
24	5289.26	54	1359.12
25	5102.04	55	2350.76
26	621.11	56	816.32
27	2596.45	57	1890.36
28	3173.97	58	1199.36
29	1451.25	59	2596.46
30	961.48	60	992

Basal Area (m^2 ha-¹)

quadrat		quadrat	
1	30.2	31	16.63
2	69.26	32	21.99
3	9.16	33	50.79
4	82.27	34	29.61
5	66.99	35	44.49
6	45.86	36	74.14
7	81.53	37	79.63
8	40.65	38	32.2
9	35.51	39	55.54
10	33.62	40	31.02
11	24.41	41	38.88
12	76.34	42	43.57
13	19.5	43	15.79
14	62.56	44	56.76
15	27.48	45	31.5
16	56.84	46	77.2
17	23.24	47	48.2
18	37.29	48	26.27
19	19.56	49	29.24
20	20.2	50	28.46
21	75.7	51	14.17
22	44.69	52	22.75
23	29.14	53	30.95
24	82.1	54	49.94
25	64.84	55	93.04
26	20.03	56	32.39
27	70.94	57	51.99
28	51.61	58	63.72
29	105.2	59	63.72
30	54.62	60	87.07

Appendix 3. Sample Scores on the First Four Axes of DCA

Quad.	Axis1	Axis2	Axis3	Axis4
1	-110	-27	-80	238
2	-109	-54	-73	-65
3	-106	-13	82	-2
4	-110	-77	44	69
5	-105	-6	-65	-111
6	-110	-77	46	69
7	-110	-80	-55	-35
8	-110	-67	-152	-32
9	-112	-100	-161	2
10	-110	-71	-55	-34
11	-106	-9	7	-48
12	-109	-58	-1	6
13	16	121	51	23
14	-106	-13	85	-1
15	-109	-63	-74	-67
16	-106	-7	-56	-101
17	-109	-61	73	62
18	-106	-13	82	-2
19	-109	-66	1	7
20	-110	-27	-80	240
21	-121	-193	313	5
22	-113	-78	202	-58
23	-106	-13	82	-3
24	-105	-6	-65	-108
25	-100	35	-167	5
26	-106	-9	9	-45
27	-106	-12	83	-2
28	-106	-13	85	-1
29	-106	-15	92	2
30	-107	-18	161	1

Quad.	Axis1	Axis2	Axis3	Axis4
31	799	-9	0	0
32	-95	45	111	179
33	-106	-9	9	-45
34	696	14	0	0
35	-108	-38	105	-38
36	-109	-57	-1	3
37	-106	-11	17	-38
38	-96	44	46	152
39	148	-125	-28	-65
40	-121	-223	-65	-35
41	115	-41	9	10
42	-34	106	73	-38
43	-105	-2	-137	-95
44	-102	-16	-68	496
45	-115	-151	-184	62
46	-113	-77	267	-2
47	-107	-17	159	1
48	-107	-16	158	0
49	29	145	-64	33
50	-112	-48	102	-24
51	-154	905	-3	0
52	-106	-10	15	-39
53	-124	329	15	-5
54	21	141	-11	-49
55	-95	48	-28	98
56	-70	67	73	-34
57	-73	26	-1	-34
58	-3	113	99	0
59	183	-132	5	0
60	189	-141	16	48

Appendix 4. Species variables codes used in the DCA

Code	Species Variable
1	*Crataegus monogyna* Frequency
2	*Crataegus monogyna* Density (ha^{-1})
3	*Crataegus monogyna* Basal area (m^2 ha^{-1})
4	*Ulmus glabra* Frequency
5	*Ulmus glabra* Density (ha^{-1})
6	*Ulmus glabra* Basal area (m^2 ha^{-1})
7	*Quercus petraea* Frequency
8	*Quercus petraea* Density (ha^{-1})
9	*Quercus petraea* Basal area (m^2 ha^{-1})
10	*Acer pseudoplatanus* Frequency
11	*Acer pseudoplatanus* Density (ha^{-1})
12	*Acer pseudoplatanus* Basal area (m^2 ha^{-1})
13	*Sorbus aucuparia*Frequency
14	*Sorbus aucuparia* Density (ha^{-1})
15	*Sorbus aucuparia* Basal area (m^2 ha^{-1})
16	*Carpinus betulus* Frequency
17	*Carpinus betulus* Density (ha^{-1})
18	*Carpinus betulus* Basal area (m^2 ha^{-1})
19	*Sambucus nigra* Frequency
20	*Sambucus nigra* Density (ha^{-1})
21	*Sambucus nigra* Basal area (m^2 ha^{-1})
22	*Betula pendula* Frequency
23	*Betula pendula* Density (ha^{-1})
24	*Betula pendula* Basal area (m^2 ha^{-1})
25	*Corylus avellana*Frequency
26	*Corylus avellana* Density (ha^{-1})
27	*Corylus avellana* Basal area (m^2 ha^{-1})
28	*Ilex aquifolium* Frequency
29	*Ilex aquifolium* Density (ha^{-1})
30	*Ilex aquifolium* Basal area (m^2 ha^{-1})
31	*Fraxinus excelsior* Frequency
32	*Fraxinus excelsior* Density (ha^{-1})
33	*Fraxinus excelsior* Basal area (m^2 ha^{-1})
34	*Fagus sylvatica* Frequency
35	*Fagus sylvatica* Density (ha^{-1})
36	*Fagus sylvatica* Basal area (m^2 ha^{-1})
37	*Ulmus procera* Frequency
38	*Ulmus procera* Density (ha^{-1})
39	*Ulmus procera* Basal area (m^2 ha^{-1})

Appendix 5.a. Tables of observed and expected numbers, plus Chi² values, for touches of total vegetation in each height category and at each distance from the woodland edge.

Observed Values

	0m	5m	10m	20m	40m	60m	totals
0-5cm	131	143	89	55	43	129	590
5-10cm	156	197	135	113	99	158	858
10-15cm	107	152	113	106	117	149	744
15-20cm	94	118	110	78	109	115	624
20-25cm	66	82	72	74	78	70	442
25-30cm	44	69	56	62	58	62	351
30-35cm	44	51	44	45	47	65	296
35-40cm	32	29	54	35	45	67	262
40-45cm	28	25	30	40	36	81	240
45-50cm	20	13	7	28	34	39	141
50-55cm	19	6	13	27	36	37	138
55-60cm	18	11	6	31	30	38	134
60-65cm	15	6	4	21	24	25	95
totals	774	902	733	715	756	1035	4915

Expected Values.

	0m	5m	10m	20m	40m	60m	totals
0-5cm	92.9115	108.276	87.9898	85.8290	90.7507	124.242	590
5-10cm	135.1154	157.46	127.958	124.815	131.973	180.677	858
10-15cm	117.163	136.538	110.956	108.231	114.438	156.671	744
15-20cm	98.26572	114.516	93.0604	90.7751	95.9804	131.408	624
20-25cm	69.60488	81.1157	65.9178	64.2990	67.9861	93.0763	442
25-30cm	55.27447	64.415	52.3464	51.0610	53.9890	73.9135	351
30-35cm	46.61322	54.3218	44.1440	43.0600	45.5292	62.3316	296
35-40cm	41.259	48.0822	39.0734	38.1139	40.2994	55.1719	262
40-45cm	37.79451	44.0447	35.7924	34.9135	36.9155	50.5391	240
45-50cm	22.20427	25.8763	21.0280	20.5117	21.6878	29.6917	141
50-55cm	21.73184	25.3257	20.5806	20.0752	21.2264	29.0600	138
55-60cm	21.10193	24.5916	19.9841	19.4933	20.6111	28.2177	134
60-65cm	14.96033	17.4343	14.1678	13.8199	14.6124	20.0050	95
totals	774	902	733	715	756	1035	4915

Chi² Values

	0m	5m	10m	20m	40m	60m	totals
0-5cm	15.6141	11.1354	0.01159	11.0735	25.1252	0.18220	63.1421
5-10cm	3.22811	9.92893	0.38753	1.11856	8.23825	2.84634	25.7477
10-15cm	0.88155	1.75078	0.03762	0.04602	0.05734	0.37563	3.14897
15-20cm	0.18517	0.10597	3.08347	1.79790	1.76607	2.04730	8.98902
20-25cm	0.18669	0.00963	0.56120	1.46359	1.47496	5.72127	9.41737
25-30cm	2.29968	0.32628	0.25499	2.34348	0.29798	1.92024	7.44268
30-35cm	0.14650	0.20313	0.00047	0.08740	0.04751	0.11423	0.59925
35-40cm	2.07782	7.57307	5.70213	0.25441	0.54826	2.53577	18.6914
40-45cm	2.53862	8.23487	0.93742	0.74103	0.02270	18.3592	30.8335
45-50cm	0.21882	6.40737	9.35829	2.73378	6.98951	2.91809	28.6258
50-55cm	0.34341	14.7472	2.79226	2.38859	10.2823	2.16941	32.7232
55-60cm	0.45597	7.51202	9.78556	6.79215	4.27679	3.39125	32.2137
60-65cm	0.00010	7.49927	7.29717	3.73035	6.03095	1.24714	25.805
totals	28.1762	75.4340	40.2097	34.5708	65.1579	43.8281	287.377

Appendix 5b. Tables of observed and expected numbers, plus Chi² values, for touches of *Rubus fruticosus* in each height category and at each distance from the woodland edge.

Observed Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	18	4	14	7	1	1	45
5 - 10 cm	28	20	36	19	2	11	116
10 - 15 cm	24	32	34	22	11	10	133
15 - 20 cm	15	27	49	25	8	10	134
20 - 25 cm	13	26	29	24	4	13	109
25 - 30 cm	12	24	31	19	4	14	104
30 - 35 cm	5	23	26	15	4	21	94
35 - 40 cm	4	16	31	9	9	12	81
40 - 45 cm	2	7	12	15	10	29	75
45 - 50 cm	3	6	6	9	8	10	42
50- 65 cm	9	11	14	12	21	38	175
totals	133	196	282	176	82	169	1108

Expected Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	5.765896	8.49711	12.22543	7.630058	3.554913	7.32659	45
5 - 10 cm	14.8632	21.90366	31.51445	19.66859	9.163776	18.88632	116
10 - 15 cm	17.04143	25.11368	36.13295	22.55106	10.50674	21.65414	133
15 - 20 cm	17.16956	25.3025	36.40462	22.72062	10.58574	21.81696	134
20 - 25 cm	13.96628	20.58189	29.61272	18.4817	8.61079	17.74663	109
25 - 30 cm	13.32563	19.63776	28.25434	17.63391	8.2158	16.93256	104
30 - 35 cm	12.04432	17.74952	25.53757	15.93834	7.425819	15.30443	94
35 - 40 cm	10.37861	15.2948	22.00578	13.7341	6.398844	13.18786	81
40 - 45 cm	9.609827	14.16185	20.37572	12.71676	5.924855	12.21098	75
45 - 50 cm	5.381503	7.930636	11.4104	7.121387	3.317919	6.83815	42
50- 65 cm	21.00632	30.95668	44.53971	27.79783	12.95126	26.69224	175
totals	140.5526	207.1301	298.0137	185.9944	86.65647	178.5969	1108

Chi ² Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	25.95838	2.380103	0.257585	0.052028	1.836214	5.463079	35.94739
5 - 10 cm	11.61093	0.165448	0.638442	0.022727	5.600278	3.293074	21.3309
10 - 15 cm	2.841415	1.88827	0.125909	0.013466	0.023157	6.272197	11.16441
15 - 20 cm	0.274147	0.113882	4.357784	0.228673	0.63161	6.400547	12.00664
20 - 25 cm	0.066854	1.426299	0.012678	1.647667	2.468924	1.269564	6.891986
25 - 30 cm	0.131873	0.969005	0.266815	0.10583	2.163267	0.507893	4.144682
30 - 35 cm	4.119984	1.553144	0.008374	0.055243	1.580463	2.119615	9.436823
35 - 40 cm	3.920245	0.032515	3.676124	1.631831	1.057381	0.106993	10.42509
40 - 45 cm	6.026067	3.62185	3.442957	0.409945	2.802904	23.08341	39.38713
45 - 50 cm	1.053898	0.469994	2.56542	0.495576	6.607118	1.461988	12.65399
50 -65 cm	6.862301	12.86537	20.94028	8.978094	5.001995	4.790362	59.4384
totals	62.86609	25.48588	36.29237	13.64108	29.77331	54.76872	222.8274

Appendix 5.c. Tables of observed and expected numbers, plus Chi² values, for touches of *Milium effusum* in each height category and at each distance from the woodland edge.

Observed Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	18	8	9	8	1	6	50
5 - 10 cm	33	12	7	26	19	17	114
10 - 15 cm	29	9	17	32	25	22	134
15 - 20 cm	34	20	8	22	22	26	132
20 - 25 cm	26	13	6	33	40	23	141
25 - 30 cm	10	11	2	21	23	26	93
30 - 45 cm	27	12	3	42	26	41	151
45 - 65 cm	12	6	4	24	26	30	102
total	189	91	56	208	182	191	917

Expected Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	10.30534	4.961832	3.053435	11.34133	9.923664	10.41439	50
5 - 10 cm	23.49618	11.31298	6.961832	25.85823	22.62595	23.74482	114
10 - 15 cm	27.61832	13.29771	8.183206	30.39477	26.59542	27.91058	134
15 - 20 cm	27.20611	13.09924	8.061069	29.94111	26.19847	27.494	132
20 - 25 cm	29.06107	13.99237	8.610687	31.98255	27.98473	29.36859	141
25 - 30 cm	19.16794	9.229008	5.679389	21.09487	18.45802	19.37077	93
30 - 45 cm	31.12214	14.98473	9.221374	34.25082	29.96947	31.45147	151
45 - 60 cm	21.0229	10.12214	6.229008	23.13631	20.24427	21.24537	102
total	189	91	56	208	182	191	917

Chi² Values

	0m	5m	10m	20m	40m	60m	totals
1 - 5 cm	5.745344	1.860294	11.58094	0.984407	8.024433	1.871149	30.06656
5 - 10 cm	3.844136	0.041722	0.000209	0.000777	0.581082	1.915896	6.383823
10 - 15 cm	0.069122	1.388984	9.499437	0.084777	0.095707	1.251674	12.3897
15 - 20 cm	1.696567	3.635367	0.000463	2.106176	0.672832	0.081183	8.192588
20 - 25 cm	0.322429	0.070381	0.791538	0.032368	5.158764	1.381032	7.756513
25 - 30 cm	4.384984	0.339843	2.38369	0.000427	1.117651	2.268708	10.4953
30 - 45 cm	0.545978	0.594514	4.197367	1.753238	0.525757	2.898891	10.51575
45 - 60 cm	3.872574	1.678698	0.797635	0.032242	1.636432	3.607546	11.62513
total	20.48113	9.609803	29.25128	4.994412	17.81266	15.27608	97.42536

Appendix 6.a. Tables of observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category of soil organic content.

Observed Values

	5-10%.	10-15%.	15-20%.	20-25%.	25-30%.	total
0-5cm	47	297	144	66	36	590
5-10cm	33	369	276	97	83	858
10-15cm	27	258	242	116	101	744
15-20cm	18	221	183	105	97	624
20-25cm	3	167	133	74	64	441
25-30cm	8	141	99	61	45	354
30-35cm	10	126	78	45	36	295
35-40cm	11	104	70	39	38	262
40-45cm	7	118	57	29	29	240
45-50cm	0	81	21	19	22	143
50-55cm	2	68	26	15	27	138
55-60cm	5	72	18	16	23	134
60-65cm	3	52	14	10	16	95
totals	174	2074	1361	692	617	4918

Expected Values

	5-10%.	10-15%.	15-20%.	20-25%.	25-30%.	total
0-5cm	20.87434	248.8125	163.2757	83.01749	74.01993	590
5-10cm	30.35624	361.8325	237.4416	120.7271	107.6425	858
10-15cm	26.3229	313.7568	205.8935	104.6865	93.34038	744
15-20cm	22.07727	263.1509	172.6848	87.80155	78.28548	624
20-25cm	15.60268	185.9768	122.0417	62.05205	55.32676	441
25-30cm	12.5246	149.2875	97.96543	49.81049	44.41196	354
30-35cm	10.43717	124.4063	81.63786	41.50874	37.00996	295
35-40cm	9.269622	110.4896	72.50549	36.86539	32.86987	262
40-45cm	8.491257	101.2119	66.41724	33.76983	30.1098	240
45-50cm	5.059374	60.30541	39.57361	20.12119	17.94042	143
50-55cm	4.882473	58.19683	38.18991	19.41765	17.31314	138
55-60cm	4.740952	56.50996	37.08296	18.85482	16.81131	134
60-65cm	3.361122	40.06303	26.29016	13.36722	11.91846	95
totals	174	2074	1361	692	617	4918

Chi² Values

	5-10%.	10-15%.	15-20%.	20-25%.	25-30%.	total
0-5cm	32.69805	9.332459	2.27562	3.48836	19.52873	67.32321
5-10cm	0.230248	0.141982	6.261525	4.663214	5.6414	16.93837
10-15cm	0.017417	9.908381	6.331832	1.222663	0.628557	18.10885
15-20cm	0.752997	6.751626	0.616167	3.368811	4.473795	15.9634
20-25cm	10.17951	1.936369	0.983965	2.300543	1.359652	16.76004
25-30cm	1.634546	0.460071	0.010926	2.513629	0.007786	4.626958
30-35cm	0.018311	0.020417	0.162107	0.293646	0.027561	0.522041
35-40cm	0.323013	0.38117	0.086579	0.1236	0.800681	1.715043
40-45cm	0.261898	2.784665	1.335263	0.673715	0.040906	5.096446
45-50cm	5.059374	7.10162	8.717398	0.062475	0.918605	21.85947
50-55cm	1.70173	1.65133	3.890923	1.005046	5.419893	13.66892
55-60cm	0.014155	4.245999	9.820127	0.43225	2.278225	16.79076
60-65cm	0.038799	3.556674	5.74542	0.848208	1.397743	11.58684
totals	52.93004	48.27276	46.23785	20.99616	42.52353	210.9603

Appendix 6.b. Tables of observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category of soil moisture content.

Observed Values

	15-25%.	25-35%.	35-45%.	45-55%.	total
0-5cm	196	216	128	48	588
5-10cm	206	323	243	67	839
10-15cm	162	288	216	53	719
15-20cm	146	236	186	43	611
20-25cm	109	192	111	18	430
25-30cm	98	135	92	26	351
30-35cm	69	120	90	14	293
35-40cm	54	107	78	23	262
40-45cm	45	99	79	17	240
45-50cm	28	60	43	12	143
50-55cm	33	45	46	14	138
55-60cm	33	52	36	12	133
60-65cm	23	34	32	6	95
totals	1202	1907	1380	353	4842

Expected Values

	5-10%.	10-15%.	15-20%.	20-25%.	total
0-5cm	145.9678	231.5812	167.5836	42.86741	588
5-10cm	208.2772	330.4364	239.1202	61.16625	839
10-15cm	178.4878	283.1749	204.9195	52.4178	719
15-20cm	151.6774	240.6396	174.1388	44.5442	611
20-25cm	106.7451	169.3536	122.5527	31.34862	430
25-30cm	87.13383	138.2398	100.0372	25.58922	351
30-35cm	72.73565	115.3967	83.50682	21.3608	293
35-40cm	65.04007	103.1875	74.67162	19.10078	262
40-45cm	59.57869	94.52292	68.40149	17.4969	240
45-50cm	35.49897	56.31991	40.75589	10.42524	143
50-55cm	34.25774	54.35068	39.33086	10.06072	138
55-60cm	33.01652	52.38145	37.90582	9.6962	133
60-65cm	23.58323	37.41532	27.07559	6.925857	95
totals	1202	. 1907	1380	353	4842

Chi² Values

	5-10%.	10-15%.	15-20%.	20-25%.	total
0-5cm	17.14915	1.048327	9.349748	0.614534	28.16175
5-10cm	0.024897	0.167354	0.062951	0.556395	0.811597
10-15cm	1.523062	0.082215	0.599155	0.006466	2.210899
15-20cm	0.21251	0.089453	0.80791	0.053532	1.163405
20-25cm	0.047631	3.028343	1.089034	5.684001	9.849009
25-30cm	1.355084	0.075927	0.645722	0.006594	2.083327
30-35cm	0.19186	0.183628	0.504886	2.536487	3.416861
35-40cm	1.873969	0.14086	0.148357	0.795982	2.959168
40-45cm	3.567351	0.212057	1.642194	0.014112	5.435713
45-50cm	1.584117	0.240467	0.123566	0.237872	2.186022
50-55cm	0.046177	1.608724	1.130855	1.542428	4.328184
55-60cm	8.27E-06	0.002778	0.095821	0.547379	0.645986
60-65cm	0.014424	0.311756	0.895634	0.12377	1.345583
totals	27.59024	7.191887	17.09583	12.71955	64.59751

Appendix 6.c. Tables of observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category of air Temperature.

Observed Values

	19-20ºc.	20-21ºc.	21-22ºc.	total
0-5cm	308	206	83	597
5-10cm	467	322	82	871
10-15cm	410	267	73	750
15-20cm	325	251	54	630
20-25cm	210	201	35	446
25-30cm	195	136	26	357
30-35cm	157	122	20	299
35-40cm	130	117	18	265
40-45cm	136	96	11	243
45-50cm	81	60	4	145
50-55cm	85	57	4	146
55-60cm	80	46	9	135
60-65cm	55	40	2	97
totals	2639	1921	421	4981

Expected Values

	19-20ºc.	20-21ºc.	21-22ºc.	total
0-5cm	316.2985	230.2423	50.45914	597
5-10cm	461.4674	335.9147	73.61795	871
10-15cm	397.36	289.2491	63.39089	750
15-20cm	333.7824	242.9693	53.24834	630
20-25cm	236.2967	172.0068	37.69645	446
25-30cm	189.1433	137.6826	30.17406	357
30-35cm	158.4142	115.314	25.27183	299
35-40cm	140.4005	102.2014	22.39811	265
40-45cm	128.7446	93.71672	20.53865	243
45-50cm	76.82293	55.9215	12.25557	145
50-55cm	77.35274	56.30717	12.34009	146
55-60cm	71.52479	52.06485	11.41036	135
60-65cm	51.39189	37.40956	8.198555	97
totals	2639	1921	421	4981

Chi² Vaues

	19-20ºc.	20-21ºc.	21-22ºc.	total
0-5cm	0.217724	2.552485	20.98544	23.75565
5-10cm	0.066332	0.576391	0.95437	1.597093
10-15cm	0.40208	1.711412	1.456599	3.570091
15-20cm	0.231079	0.265434	0.01061	0.507124
20-25cm	2.926481	4.887039	0.192878	8.006399
25-30cm	0.181346	0.020563	0.577409	0.779318
30-35cm	0.012624	0.387661	1.099731	1.500016
35-40cm	0.770445	2.142825	0.863617	3.776887
40-45cm	0.408875	0.055629	4.429979	4.894483
45-50cm	0.227119	0.297455	5.5611	6.085674
50-55cm	0.756025	0.008525	5.636679	6.401229
55-60cm	1.004255	0.706472	0.509172	2.219899
60-65cm	0.253317	0.179377	4.686445	5.119139
totals	7.457701	13.79127	46.96403	68.213

Appendix 6.d. Tables of observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category of soil temperature.

Observed Values

	12-13ºc.	13-14ºc.	14-15ºc.	15-16ºc.	total
0-5cm	31	78	304	161	574
5-10cm	38	205	417	160	820
10-15cm	36	222	316	128	702
15-20cm	30	213	248	110	601
20-25cm	18	156	166	82	422
25-30cm	7	135	145	63	350
30-35cm	9	107	125	51	292
35-40cm	11	96	107	47	261
40-45cm	10	91	106	32	239
45-50cm	2	66	51	24	143
50-55cm	5	56	51	26	138
55-60cm	3	51	52	27	133
60-65cm	1	39	39	16	95
totals	201	1515	2127	927	4770

Expected Values

	12-13ºc.	13-14ºc.	14-15ºc.	15-16ºc.	total
0-5cm	24.18742	182.3082	255.9535	111.5509	574
5-10cm	34.55346	260.4403	365.6478	159.3585	820
10-15cm	29.58113	222.9623	313.0302	136.4264	702
15-20cm	25.32516	190.8836	267.9931	116.7981	601
20-25cm	17.78239	134.0314	188.1748	82.01132	422
25-30cm	14.74843	111.1635	156.0692	68.01887	350
30-35cm	12.3044	92.74214	130.2063	56.74717	292
35-40cm	10.99811	82.89623	116.383	50.72264	261
40-45cm	10.07107	75.90881	106.573	46.44717	239
45-50cm	6.025786	45.41824	63.76541	27.79057	143
50-55cm	5.815094	43.83019	61.53585	26.81887	138
55-60cm	5.604403	42.24214	59.30629	25.84717	133
60-65cm	4.003145	30.17296	42.36164	18.46226	95
totals	201	1515	2127	927	4770

Chi² Values

	12-13ºc.	13-14ºc.	14-15ºc.	15-16ºc.	total
0-5cm	1.918817	59.68024	9.019101	21.92011	92.53827
5-10cm	0.343776	11.80164	7.211991	0.002582	19.35999
10-15cm	1.392843	0.004153	0.028175	0.52046	1.945631
15-20cm	0.862943	2.562467	1.491543	0.395677	5.31263
20-25cm	0.002663	3.600777	2.613121	1.56E-06	6.216563
25-30cm	4.070816	5.111188	0.78508	0.370324	10.33741
30-35cm	0.887412	2.191955	0.208173	0.582055	3.869595
35-40cm	3.24E-07	2.071372	0.756477	0.273213	3.101061
40-45cm	0.000502	3.000234	0.00308	4.493723	7.497539
45-50cm	2.6896	9.326845	2.55555	0.517024	15.08902
50-55cm	0.114251	3.379048	1.803893	0.025003	5.322195
55-60cm	1.210283	1.815726	0.900105	0.051418	3.977532
60-65cm	2.252948	2.582336	0.266765	0.328386	5.430435
totals	15.74685	107.128	27.64305	29.47998	179.9979

Appendix 6.e. Tablesof observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category Illumination.

Observed Values

	1-20Lux.	20-40Lux.	40-60Lux.	60-80Lux.	80-100Lux	total
0-5cm	259	180	42	59	50	590
5-10cm	427	270	57	59	45	858
10-15cm	399	205	52	56	32	744
15-20cm	321	184	59	40	20	624
20-25cm	248	118	51	15	9	441
25-30cm	170	120	42	13	9	354
30-35cm	127	97	41	14	16	295
35-40cm	96	116	20	19	11	262
40-45cm	101	90	20	19	10	240
45-50cm	64	50	12	8	9	143
50-55cm	63	55	9	7	4	138
55-60cm	61	47	8	12	6	134
60-65cm	49	33	2	4	7	95
totals	2385	1565	415	325	228	4918

Expected Values

	1-20Lux.	20-40Lux.	40-60Lux.	60-80Lux.	80-100Lux	total
0-5cm	286.1224	187.7491	49.7865	38.98943	27.35258	590
5-10cm	416.0899	273.0317	72.40138	56.69988	39.77715	858
10-15cm	360.8052	236.7548	62.78162	49.16633	34.49207	744
15-20cm	302.6108	198.5685	52.65555	41.23627	28.92883	624
20-25cm	213.8644	140.3345	37.2133	29.14294	20.4449	441
25-30cm	171.6734	112.6495	29.8719	23.39366	16.41155	354
30-35cm	143.0612	93.87454	24.89325	19.49471	13.67629	295
35-40cm	127.0577	83.37332	22.10858	17.31395	12.1464	262
40-45cm	116.3888	76.37251	20.25214	15.86011	11.12647	240
45-50cm	69.34831	45.50529	12.0669	9.44998	6.629524	143
50-55cm	66.92355	43.91419	11.64498	9.119561	6.397723	138
55-60cm	64.98373	42.64132	11.30744	8.855226	6.212281	134
60-65cm	46.07056	30.23078	8.01647	6.277959	4.404229	95
totals	2385	1565	415	325	228	4918

Chi² Values

	1-20Lux.	20-40Lux.	40-60Lux.	60-80Lux.	80-100Lux	total
0-5cm	2.571015	0.319833	1.217791	10.27004	18.75163	33.13031
5-10cm	0.28607	0.033664	3.276216	0.093308	0.685776	4.375034
10-15cm	4.043296	4.259116	1.85155	0.949818	0.180053	11.28383
15-20cm	1.117482	1.06886	0.76444	0.037064	2.755868	5.743714
20-25cm	5.448504	3.554574	5.107667	6.863509	6.406765	27.38102
25-30cm	0.016312	0.479635	4.924054	4.617837	3.347098	13.38494
30-35cm	1.80316	0.104059	10.4216	1.548721	0.394816	14.27235
35-40cm	7.591695	12.76787	0.201103	0.16419	0.1082	20.83306
40-45cm	2.034684	2.431615	0.003139	0.621619	0.114047	5.205104
45-50cm	0.412475	0.443958	0.000371	0.222481	0.847596	1.926881
50-55cm	0.230027	2.798529	0.600766	0.492627	0.898613	5.020561
55-60cm	0.244217	0.445533	0.967431	1.11681	0.007254	2.781245
60-65cm	0.186272	0.253667	4.515443	0.826558	1.529899	7.311838
totals	25.98521	28.96091	33.85157	27.82458	36.02762	152.6499

Appendix 6.f. Table of observed and expected numbers plus Chi² values for touches of total vegetation, in each height category, within each category of P.A.R.

Observed Values

	10-30μEm^{-2}S^{-1}	30-50μE m^{-2}S^{-1}.	50-100μE m^{-2}S^{-1}.	100-200μE m^{-2}S^{-1}.	200-300μE m^{-2}S^{-1}.	totals
0-5cm	91	170	172	83	74	590
5-10cm	141	266	279	115	57	858
10-15cm	137	243	218	103	43	744
15-20cm	95	210	193	102	24	624
20-25cm	76	155	131	69	10	441
25-30cm	44	112	133	53	12	354
30-35cm	57	69	96	54	19	295
35-40cm	36	60	112	37	17	262
40-45cm	47	52	90	36	15	240
45-50cm	32	32	49	21	9	143
50-55cm	32	34	51	17	4	138
55-60cm	30	38	40	18	8	134
60-65cm	22	34	26	5	8	95
totals	840	1475	1590	713	300	4918

Expected Values

	10-30μEm^{-2}S^{-1}	30-50μE m^{-2}S^{-1}.	50-100μE m^{-2}S^{-1}.	100-200μE m^{-2}S^{-1}.	200-300μE m^{-2}S^{-1}.	totals
0-5cm	100.7727	176.952	190.7483	85.5368	35.99024	590
5-10cm	146.5474	257.3302	277.3932	124.3908	52.33835	858
10-15cm	127.076	223.1395	240.5368	107.8634	45.3843	744
15-20cm	106.5799	187.1492	201.7405	90.46604	38.06425	624
20-25cm	75.3233	132.2641	142.5763	63.93514	26.90118	441
25-30cm	60.4636	106.1712	114.449	51.32208	21.59414	354
30-35cm	50.38634	88.47601	95.37414	42.7684	17.99512	295
35-40cm	44.7499	78.57869	84.70516	37.98414	15.98211	262
40-45cm	40.99227	71.98048	77.59252	34.79463	14.6401	240
45-50cm	24.42456	42.88837	46.23221	20.7318	8.723058	143
50-55cm	23.57056	41.38878	44.6157	20.00691	8.418056	138
55-60cm	22.88735	40.1891	43.32249	19.427	8.174054	134
60-65cm	16.22611	28.49227	30.7137	13.77288	5.795039	95
totals	840	1475	1590	713	300	4918

Chi² Values

	10-30μEm^{-2}S^{-1}	30-50μE m^{-2}S^{-1}.	50-100μE m^{-2}S^{-1}.	100-200μE m^{-2}S^{-1}.	200-300μE m^{-2}S^{-1}.	totals
0-5cm	0.947728	0.273128	1.842731	0.075235	40.1426	43.28142
5-10cm	0.209989	0.292096	0.009307	0.708953	0.415202	1.635548
10-15cm	0.775007	1.767683	2.111558	0.21928	0.125261	4.99879
15-20cm	1.258158	2.790056	0.37869	1.47052	5.196561	11.09399
20-25cm	0.006079	3.908238	0.939915	0.401232	10.61849	15.87395
25-30cm	4.482866	0.32	3.006938	0.054858	4.262619	12.12728
30-35cm	0.868103	4.287206	0.004107	2.949579	0.056114	8.16511
35-40cm	1.710858	4.392638	8.795308	0.025498	0.064829	14.98913
40-45cm	0.880478	5.54622	1.984027	0.041757	0.008848	8.461329
45-50cm	2.349571	2.764306	0.1657	0.00347	0.008792	5.291839
50-55cm	3.014588	1.319053	0.913565	0.45192	2.318732	8.017858
55-60cm	2.21038	0.11924	0.254808	0.10482	0.003706	2.692955
60-65cm	2.054579	1.064676	0.723423	5.588037	0.838968	10.26968
totals	20.76839	28.84454	21.13008	12.09516	64.06072	146.8989

Appendix 7. Species codes for the CCA.

Code	Species name	Code	Species name
1	*Lamium album*	32	*Taraxicum vulgaris*
2	*Anthriscus sylvaticum*	33	*Deschampsia cespitosa*
3	*Geum urbanum*	34	*Cerastium fontanum*
4	*Hedera helix*	35	*Dactylus glomeratus*
5	*Geranium robertianum*	36	*Conopodium majus*
6	*Rumex sanguineus*	37	*Heracleum sphondylium*
7	*Milium effusum*	38	*Ranunculus ficaria*
8	*Galium aparine*	39	*Carpinus betula* seedling
9	*Rubus fruticosus*	40	*Sambucus nigra* seedling
10	*Mnium hornum*	41	*Galium odoratum*
11	*Aegopodium podagaria*	42	*Holcus mollis*
12	*Agrostis stolonifera*	43	*Lolium perenne*
13	*Hyacinthoides non-scriptus*	44	*Fraxinus excelsior* seedling
14	*Veronica montana*	45	*Bromus ramosus*
15	*Arun maculatum*	46	*Urtica diocia*
16	*Ranunculus repens*	47	*Anemone nemorosa*
17	*Acer pseudoplatanus* seedling	48	*Lonicera periclymenum*
18	*Quercus petraea* seedling	49	*Dryopteris carthusiana*
19	*Ilex aquifolium*	50	*Ulmus glabra* seedling
20	*Oxalis acetosella*	51	*Carpinus betulus*
21	*Sambucus nigra*	52	*Epilobium* spp.
22	*Taxus baccata*	53	*Dryopteris dilatata*
23	*Eurhyncium praelongum*	54	*Chryosplenium oppositofolium*
24	*Rumex acetosa*	55	*Geranium sylvaticum*
25	*Holcus lanatus*	56	*Viola riviniana*
26	*Stellaria media*	57	*Valerium officinalis*
27	*Rosa canina*	58	*Silene dioica*
28	*Crataegus monogyna*	59	*Cirriphyllum piliferum*
29	*Brachythesium rutabulum*	60	*Deschampsia flexuosa*
30	*Stachys sylvatica*	61	*Mercurialis perennis*
31	*Stellaria graminea*		

Appendix 8 Ranked correlation of species domin scores and environmental variables (s=seedling).

	Lamium album	*Anthriscus sylvestris*	*Geum urbanum*	*Hedera helix*	*Geranium robertianum*	*Rumex sanguineus*	*Milium effusum*	*Galium aparine*	*Rubus fruticosus*	*Mnium hornum.*	*Aegopodium podagaria*	*Agrostis stolonifera*	*H. non-scriptus*
Lamium album	1												
Anthriscus sylvestris	0.152184	1											
Geum urbanum	0.361898	0.406063	1										
Hedera helix	-0.03429	0.151345	-0.14876	1									
Geranium robertianum	0.07745	0.213014	0.266854	-0.07745	1								
Rumex sanguineus	0.385219	0.524724	0.525348	-0.06454	0.241036	1							
Milium effusum	0.048308	0.114138	0.074995	-0.0858	-0.07276	0.160508	1						
Galium aparine	0.078209	0.057527	0.266068	0.175	0.368507	0.241077	0.118697	1					
Rubus fruticosus	-0.12185	0.149379	-0.01829	-0.07598	-0.14155	-0.03886	0.322119	-0.16265	1				
Mnium hornum.	0.237993	0.116705	0.148172	0.265311	0.056166	0.303618	0.074934	-0.05623	-0.15184	1			
Aegopodium podagaria	0.060567	0.01782	0.172381	-0.04858	0.029573	-0.06516	-0.05914	-0.10303	0.040129	0.313517	1		
Agrostis stolonifera	-8.50E-18	0.060189	0.278376	-0.20475	-0.03396	0.18621	0.121583	0.030158	-0.07982	0.305909	0.158098	1	
H. non-scriptus	-0.03448	0.101456	0.055205	0.043142	0.094287	0.356685	0.121503	-0.01955	0.055848	0.733813	0.302836	0.409136	1
Veronica montana	-0.02195	0.045198	0.2635	0.063361	0.156444	0.297825	0.219869	0.43552	-0.01777	0.151463	-0.10793	0.158833	0.175564
Arum maculatum	0.195402	-0.05073	0.193217	-0.14491	0.094287	-0.01427	0.121503	0.175971	0.055848	0.039666	0.060567	0.245481	-0.03448
Ranunculus repens	0.095349	0.05395	0.082195	-0.14753	0.032947	0.221532	0.180907	0.20794	-0.04644	-0.08859	-0.09018	0.282827	-0.05134
A. Pseudo-platanus (s)	-0.05015	-0.14085	0.031628	-0.09083	-0.18565	-0.17543	0.122515	-0.14735	0.139957	-0.06031	-0.07207	-0.1136	-0.09574
Quercus Petraea	0.137931	-0.05073	-0.08281	-0.02323	0.043776	-0.07134	-0.09808	-0.13687	-0.05839	0.039666	0.302836	-0.08183	-0.03448
Ilex aquifolium	-0.07119	-0.10473	-0.125	-0.14962	0.177832	-0.13587	-0.21418	0.022136	-0.1814	-0.07	-0.12504	-0.10354	-0.07119
Oxalis acetosella	-0.20457	-0.23911	-0.13609	-0.02994	-0.01532	-0.29799	0.032002	0.007945	0.309657	-0.15151	-0.14274	-0.19617	-0.20457
Sambucus nigra	-0.05181	-0.07622	0.104213	-0.09627	0.1008	0.387509	0.197785	0.038416	-0.05252	0.391967	-0.091	0.302633	0.545999
Taxus baccata	-0.02418	-0.03556	-0.09031	0.262912	-0.11096	-0.05001	-0.00718	-0.09596	-0.14772	0.375423	-0.04246	0.114736	-0.02418

Veronica montana	*Arum maculatum*	*Ranunculus repens*	*A. pseudo-platanus (s)*	*Quercus patraea*	*Ilex aquifolium*	*Oxalis acetosella*	*Sambucus nigra*	*Taxus baccata*	*Eurhynkium praelongum*	*Rumex acetosa*	*Holcus lanatus*	*Stellaria media*	*Rosa canina*
1													
0.263345	1												
0.261398	0.53542	1											
-0.06964	0.132214	0.090184	1										
-0.08778	-0.03448	-0.05134	-0.09574	1									
-0.0338	-0.07119	-0.06203	-0.0337	-0.07119	1								
-0.11414	-0.05044	-0.21518	0.08781	-0.16254	0.047962	1							
0.172474	-0.05181	0.024583	0.172304	-0.05181	-0.07511	-0.05474	1						
-0.06154	-0.02418	-0.036	-0.06712	-0.02418	-0.04991	-0.14342	0.29897	1					

Eurhinkium praelongum	-0.11668	0.050713	0.285845	0.163839	-0.08105	0.193099	0.279406	0.145846	-0.18877	0.050329	-0.1211	0.223383	0.082203
Rumex acetosa	-0.03929	-0.05781	0.097855	-0.12732	-0.1036	-0.08129	-0.19517	-0.02228	-0.12439	-0.0678	0.023006	0.25642	-0.03929
Holcus lanatus	-0.06577	-0.09676	0.118296	0.016645	-0.00214	-0.07559	-0.29877	0.070444	-0.08985	-0.11349	0.243885	0.086709	-0.06577
Stellaria media	-0.03448	-0.05073	0.055205	-0.18916	-0.15827	0.014267	-0.05416	-0.07821	-0.24878	-0.0595	-0.06057	0.531876	-0.03448
Rosa canina	-0.06034	-0.08877	-0.03898	0.228312	-0.05365	-0.12483	0.030604	0.106243	0.05915	-0.10411	-0.10598	-0.10927	-0.06034
Ctataegus monogyna	-0.05333	-0.01961	0.138736	-0.01026	-0.14712	0.187552	-0.01585	0.083155	-0.04613	0.023004	-0.09367	0.371735	0.146654
B. rutabulum	-0.05288	0.077787	-0.00941	0.252745	0.092945	-0.10939	-0.01571	-0.02998	-0.07007	-0.09124	-0.09287	-0.12547	-0.05288
Stachys sylvatica	-0.0491	-0.01032	-0.03369	0.081674	0.144516	0.159605	0.05687	0.198842	-0.10636	-0.08471	-0.08623	-0.04161	-0.0491
Stellaria graminea	-0.07871	-0.09053	0.202392	-0.01446	0.137664	-0.07757	-0.35148	0.296199	0.012116	-0.13582	0.173452	-0.18679	-0.07871
Taraxacum Vulgaris	-0.05288	0.272255	0.378582	-0.05258	0.054218	0.240655	0.118972	0.149909	0.046711	-0.09124	3.74E-17	0.282318	-0.05288
Deschampsia cespitosa	-0.04808	-0.0101	0.260228	-0.16459	0.222004	0.002842	-0.18923	0.112937	-0.0359	-0.08296	0.349845	-0.11409	-0.04808
Cerastium fontanum	-0.02418	-0.03556	-0.09031	-0.01629	-0.04013	-0.05001	-0.00718	-0.01371	-0.09433	-0.04171	-0.04246	-0.05737	-0.02418
Dactylis glomeratus	-0.07835	0.295924	0.159325	-0.05278	0.099459	0.342554	0.19785	0.222115	-0.03445	-0.13518	-0.09298	0.077882	-0.07835
Conopodium majus	-0.04661	-0.06856	0.214515	-0.02018	0.195706	-0.09642	0.000989	0.310512	0.088349	-0.08042	-7.70E-18	-0.1106	-0.04661
Heracleum sphondylium	-0.05599	-0.08237	0.179271	0.242479	0.005468	-0.06023	-0.04516	0.234927	-0.02061	0.096607	-0.01967	-0.13286	-0.05599
Ranunculus ficaria	-0.07052	0.320661	0.343827	0.04504	0.192824	0.379314	0.085187	0.265362	0.057579	0.210173	0.078823	0.072262	0.217971
Carpinus betulus (s)	-0.03448	-0.05073	0.055205	0.043142	0.195308	-0.07134	-0.09808	0.097761	0.055848	-0.0595	-0.06057	-0.08183	-0.03448
Sambucus nigra (s)	-0.02418	-0.03556	-0.09031	0.07678	0.172341	-0.05001	-0.19192	-0.09596	-0.04093	-0.04171	-0.04246	-0.05737	-0.02418
Galium odoratum	-0.02418	-0.03556	-0.09031	0.262912	-0.11096	-0.05001	-0.19192	0.068539	0.172635	-0.04171	-0.04246	-0.05737	-0.02418
Holcus mollis	-0.09973	-0.14672	-0.16947	-0.18843	-0.16941	-0.19329	0.047242	-0.33335	0.465837	-0.17208	-0.11986	-0.15259	-0.09973
Lolium perenne	-0.02418	-0.03556	-0.09031	-0.10935	0.172341	-0.05001	0.115974	0.068539	0.012458	-0.04171	-0.04246	-0.05737	-0.02418
Fraxinus excelsior	-0.02418	-0.03556	0.232221	-0.15589	0.101516	-0.05001	0.054395	-0.09596	0.119243	-0.04171	0.127389	0.200788	-0.02418
Bromus ramosus	-0.06337	0.509181	0.374614	0.098055	0.266115	0.449795	0.167426	0.063576	-0.04271	0.227109	-0.11131	-0.01157	0.229121
Urtica dioica	-0.05383	0.110867	0.086179	0.093252	0.076223	0.222725	0.162253	0.289966	-0.04954	-0.09288	-0.09455	-0.0511	-0.05383
Anemone nemorosa	-0.03935	-0.00827	-0.10201	0.157449	-0.03239	-0.0535	0.117187	-0.09882	0.21894	-0.0679	-0.06912	-0.05336	-0.03935

0.290266	-0.05038	0.105472	-0.03997	-0.11668	-0.06075	-0.1168	0.146495	-0.0818	1				
-0.10003	-0.03929	-0.0585	-0.05715	-0.03929	-0.08112	0.086219	-0.05904	-0.02755	0.048347	1			
-0.11162	0.056028	-0.03575	-0.06667	-0.06577	-0.11632	0.239342	0.036319	-0.04611	-0.05395	0.313672	1		
-0.08778	-0.03448	0.278712	-0.09574	-0.03448	-0.0023	-0.1205	-0.05181	-0.02418	0.400408	0.550113	0.080388	1	
-0.1051	-0.06034	-0.00878	-0.04157	-0.06034	-0.11188	0.230473	0.041476	-0.0423	0.16216	-0.06876	0.450269	-0.06034	1
0.220605	-0.05333	0.303427	-0.09519	-0.05333	-0.03019	-0.15385	0.151006	-0.03739	0.465457	-0.06077	0.011302	0.546618	0.01719
0.134606	-0.05288	-0.07873	-0.0769	-0.05288	-0.10916	0.116022	-0.07945	-0.03707	0.085389	-0.06025	0.04856	-0.05288	0.053563
0.276743	-0.0491	0.374443	-0.08067	-0.0491	-0.07333	0.067828	0.023508	-0.03442	-0.03668	-0.05595	0.382006	-0.0491	0.321032
-0.14573	0.021468	-0.04414	-0.01419	-0.07871	-0.1625	0.269254	-0.03887	-0.05519	-0.1871	0.334326	0.498948	-0.07871	0.178601
0.269211	-0.05288	0.118092	-0.00699	-0.05288	-0.09155	-0.20626	0.042779	-0.03707	0.248036	-0.06025	-0.02615	0.079314	0.00487
-0.04371	0.157968	0.01607	0.029966	-0.04808	-0.09925	0.23387	0.02302	-0.03371	-0.05176	0.023479	0.403197	-0.04808	0.143588
-0.06154	-0.02418	0.272534	0.316436	-0.02418	-0.04991	0.151281	0.29897	-0.01695	0.085518	-0.02755	0.15883	-0.02418	0.224877
0.439309	-0.07835	0.410297	-0.06635	-0.07835	0.015934	-0.26861	-0.05898	-0.05493	0.257596	0.127881	-0.05968	0.175747	-0.09029
-0.05191	-0.04661	-0.06939	0.009243	-0.04661	-0.0031	0.19222	0.010773	-0.03268	-0.11738	0.212435	0.10865	-0.04661	0.304756
0.413338	0.055989	-0.08336	0.288699	-0.05599	0.063387	0.159254	-0.08412	-0.03925	0.146389	0.191403	0.083061	-0.05599	-0.09797
0.591603	0.121807	-0.04364	-0.0178	-0.07052	0.02092	-0.0198	0.271929	-0.04944	0.234666	-0.08036	0.096466	-0.07052	-0.10569
-0.08778	-0.03448	-0.05134	-0.09574	0.482759	-0.07119	0.04764	-0.05181	-0.02418	-0.11668	-0.03929	-0.06577	-0.03448	0.320755
-0.06154	-0.02418	-0.036	-0.06712	0.701089	-0.04991	-0.08448	-0.03632	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
-0.06154	-0.02418	-0.036	-0.06712	-0.02418	-0.04991	0.09234	-0.03632	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
-0.16369	-0.09973	-0.14849	-0.00625	-0.09973	-0.00664	0.355343	-0.14985	-0.06992	-0.31324	-0.00897	-0.19023	-0.09973	-0.17452
-0.06154	-0.02418	-0.036	0.124657	-0.02418	-0.04991	0.09234	0.131323	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
0.2154	-0.02418	-0.036	-0.06712	-0.02418	-0.04991	-0.14342	-0.03632	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
0.378503	0.034124	0.123391	-0.05994	-0.06337	-0.05292	-0.09072	0.242836	-0.04443	0.336641	-0.07222	-0.12088	-0.06337	-0.1109
0.3974	-0.05383	0.349219	-0.06405	-0.05383	0.060942	-0.31935	-0.08088	-0.03774	0.190418	-0.06134	-0.10268	-0.05383	-0.0942
-0.01431	-0.03935	-0.05859	0.024529	-0.03935	0.098466	0.177728	-0.05913	-0.02759	-0.09425	-0.04484	-0.07506	-0.03935	-0.06886

Crataegus monogyna	*B. rutabulum*	*Stachys sylvatica*	*Stellaria graminea*	*Taraxacum Vulgaris*	*D. cespitosa*	*Cerastium fontanum*	*Dactylis glomeratus*	*Conopodium majus*	*Heracleum sphondylium*	*Ranunculus ficaria*	*Carpinus betulus (s)*	*Sambucus nigra (s)*	*Galium odoratum*
1													
0.122662	1												
-0.03525	0.193586	1											
-0.12173	-0.03292	0.062585	1										
0.22488	-0.08108	-0.07528	-0.03292	1									
-0.07435	0.136913	0.015367	0.523083	0.031595	1								
-0.03739	-0.03707	-0.03442	0.185626	0.333639	0.255206	1							
0.050757	-0.12014	0.340664	-0.08393	0.253258	-0.05862	0.123214	1						
-0.07208	-0.07147	-0.06636	0.357856	-0.07147	0.143885	-0.03268	0.001431	1					
0.043295	-0.08585	-0.07972	0.151046	-0.08585	-0.07806	-0.03925	0.244102	0.264859	1				
0.225559	-0.10814	-0.06129	0.006652	0.113052	0.246444	-0.04944	0.300367	0.002166	0.447601	1			
-0.05333	-0.05288	-0.0491	0.093027	-0.05288	0.157968	-0.02418	-0.07835	0.477714	-0.05599	-0.07052	1		
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	-0.03925	-0.04944	0.701089	1	
-0.03739	-0.03707	-0.03442	0.06522	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	-0.03925	-0.04944	-0.02418	-0.01695	1
-0.09336	0.068417	-0.142	-0.0708	0.028172	-0.02927	-0.06992	-0.13957	-0.1348	-0.08523	-0.20396	-0.09973	-0.06992	0.095682
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	0.457452	-0.03925	-0.04944	-0.02418	-0.01695	-0.01695
-0.03739	-0.03707	-0.03442	-0.05519	0.518993	-0.03371	-0.01695	0.212285	-0.03268	-0.03925	-0.04944	-0.02418	-0.01695	-0.01695
0.015078	0.201832	0.177484	-0.09611	-0.09718	0.028158	-0.04443	0.394839	-0.03624	0.182053	0.522951	-0.06337	-0.04443	-0.04443
0.041625	-0.08254	0.416055	-0.07596	0.165088	-0.07505	-0.03774	0.65118	0.036378	0.122365	0.295235	-0.05383	-0.03774	-0.03774
0.004347	0.025862	-0.05603	-0.08983	0.068966	-0.05487	-0.02759	-0.08941	-0.05319	0.045642	0.013588	-0.03935	-0.02759	-0.02759

Holcus mollis	*Lolium perenne*	*Fraxinus excelsior*	*Bromus ramosus*	*Urtica dioica*	*Anemone nemorosa*	*Lonicera pe-riclymenum*	*Dryopteris carthusiana*	*Ulmus glabra (s)*	*Carpinus betulus*	*Epilobium spp.*	*Dryopteris dilatata*	*Geranium sylvaticum*	*Viola riviniana*
1													
-0.06992	1												
0.261286	-0.01695	1											
-0.18329	-0.04443	-0.04443	1										
-0.15569	-0.03774	-0.03774	0.380507	1									
0.219941	-0.02759	-0.02759	-0.07233	0.043882	1								

Lonicera periclymenum	-0.06604	-0.09715	-0.2467	-0.17161	-0.29707	-0.12638	0.106539	-0.19893	0.147981	-0.06647	-0.116	-0.15672	-0.06604
Dryopteris carthusiana	-0.0426	0.062672	-0.00758	-0.00137	0.386899	-0.08813	-0.19352	-0.07247	-0.38575	-0.07351	-0.07483	-0.10109	-0.0426
Ulmus glabra	-0.03929	-0.05781	0.062907	0.225639	0.011512	-0.01626	0.155137	-0.02228	-0.05207	0.158199	-0.06902	-0.02331	-0.03929
Carpinus betulus	-0.02943	-0.0433	-0.07854	0.025495	-0.06611	-0.06089	0.291154	-0.07677	0.015168	-0.05079	-0.0517	-0.00698	-0.02943
Epilobium spp.	-0.02418	-0.03556	0.038704	-0.01629	0.172341	-0.05001	0.239132	0.068539	0.012458	-0.04171	-0.04246	0.200788	-0.02418
Dryopteris dilatata	-0.07801	-0.11476	-0.17399	0.317047	0.104891	-0.08193	0.099095	0.098671	0.035782	0.014955	-0.13702	-0.16375	-0.07801
Geranium sylvaticum	-0.02418	-0.03556	0.232221	0.169846	0.101516	0.070019	-0.00718	0.068539	-0.20111	0.375423	-0.04246	-0.05737	-0.02418
Viola riviniana	-0.02418	-0.03556	0.232221	0.169846	0.101516	0.070019	-0.00718	0.068539	-0.20111	0.375423	-0.04246	-0.05737	-0.02418
Impatiens balsamifera	-0.04798	-0.07059	-0.17925	0.266069	-0.09047	-0.09927	0.267796	0.261614	0.016575	-0.08279	-0.08428	-0.11387	-0.04798
Valeriana officinalis	-0.02943	-0.0433	0.204201	0.172801	0.071861	0.056022	0.021243	0.123506	-0.17985	0.355517	-0.0517	-0.06985	-0.02943
Silene dioica	-0.02418	-0.03556	-0.09031	0.216379	0.101516	-0.05001	0.239132	0.315282	-0.04093	-0.04171	-0.04246	-0.05737	-0.02418
Cirriphylum piliferum	-0.03002	-0.04417	-0.11215	-0.09085	-0.07916	-0.06211	0.059052	-0.00567	-0.20554	-0.0518	-0.05273	-0.07124	-0.03002
D. Flexuosa	-0.02418	-0.03556	-0.09031	-0.15589	-0.11096	-0.05001	0.300712	-0.01371	0.06585	-0.04171	-0.04246	-0.05737	-0.02418
Mercurialis perennis	-0.03448	-0.05073	0.147213	0.043142	-0.00673	-0.07134	0.121503	0.039105	-0.05839	-0.0595	-0.06057	-0.08183	-0.03448
C. oppositifolium	-0.02418	-0.03556	-0.09031	-0.01629	0.101516	0.310084	0.115974	0.233034	-0.09433	-0.04171	-0.04246	-0.05737	-0.02418
organic content	0.064597	0.186637	0.13722	0.358149	0.058486	0.319765	0.112405	0.137074	-0.21784	0.331702	-0.01414	-0.01677	0.214906
moisture content	-0.07863	0.075716	-0.0906	-0.02941	0.2445	-0.04481	-0.10629	0.026752	-0.07341	0.104841	0.234166	0.227093	0.128671
air temperature	-0.29845	0.031548	-0.15974	-0.05039	-0.14921	-0.0386	0.125409	-0.17389	0.153138	-0.2251	-0.17139	-0.40266	-0.12331
soil temperature	-0.30559	-0.20506	-0.33474	-0.02459	-0.05393	-0.14685	-0.00706	-0.0079	0.13222	-0.28985	-0.32206	-0.12977	-0.04289
illumination	-0.16441	-0.09307	-0.06819	-0.04317	0.003141	0.005767	0.066233	0.268732	0.086436	-0.28677	-0.11112	-0.31742	-0.2359
P.A.R.	-0.25198	0.129348	0.068188	0.100271	0.032984	0.054569	0.0066	0.185437	-0.13617	-0.17268	-0.18896	-0.04008	-0.12867

-0.15236	-0.06604	-0.09833	0.242301	-0.06604	0.366686	0.171745	-0.09923	-0.0463	-0.16632	-0.07526	-0.12597	-0.06604	-0.11556
0.054225	-0.0426	-0.06343	-0.11828	-0.0426	0.195757	-0.07963	-0.06401	-0.02987	-0.0131	-0.04855	-0.08126	-0.0426	-0.07455
0.100029	0.091686	-0.0585	0.046757	-0.03929	-0.05495	0.277818	0.03179	-0.02755	0.350514	-0.04478	-0.01943	-0.03929	0.401695
-0.07493	-0.02943	-0.04383	-0.03502	-0.02943	-0.03724	0.141133	0.037422	-0.02064	-0.08601	-0.03354	-0.00624	-0.02943	-0.01898
-0.06154	-0.02418	-0.036	0.124657	-0.02418	0.046689	0.210221	0.29897	-0.01695	-0.02603	-0.02755	0.15883	-0.02418	0.091287
0.015276	0.002	-0.11615	-0.12138	-0.07801	0.062739	0.312586	-0.08946	-0.05469	0.128281	-0.08889	-0.13183	-0.07801	0.117713
0.307714	0.217579	-0.036	0.124657	-0.02418	-0.04991	0.269161	-0.03632	-0.01695	0.197063	-0.02755	-0.04611	-0.02418	-0.0423
0.307714	0.217579	-0.036	0.124657	-0.02418	-0.04991	0.269161	-0.03632	-0.01695	0.197063	-0.02755	-0.04611	-0.02418	-0.0423
0.216115	-0.04798	-0.07144	-0.13323	-0.04798	-0.09906	0.129285	-0.0721	-0.03364	0.408167	-0.05468	-0.09152	-0.04798	0.242378
0.419614	0.206043	-0.04383	0.105075	-0.02943	-0.06077	0.284658	-0.04423	-0.02064	0.239933	-0.03354	-0.05614	-0.02943	-0.05151
-0.06154	-0.02418	-0.036	-0.06712	-0.02418	-0.04991	0.09234	-0.03632	-0.01695	0.197063	-0.02755	-0.04611	-0.02418	0.091287
-0.07642	-0.03002	-0.0447	-0.08335	-0.03002	-0.06198	-0.05611	-0.04511	-0.02105	-0.02463	-0.03421	-0.05726	-0.03002	-0.01567
-0.06154	-0.02418	-0.036	0.124657	-0.02418	-0.04991	0.0334	-0.03632	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
0.109727	-0.03448	-0.05134	0.041032	-0.03448	0.204379	-0.20457	-0.05181	-0.02418	0.360632	-0.03929	-0.06577	-0.03448	-0.06034
0.307714	-0.02418	0.581063	-0.06712	-0.02418	-0.04991	-0.14342	-0.03632	-0.01695	-0.0818	-0.02755	-0.04611	-0.02418	-0.0423
0.239604	-0.0535	0.050506	-0.0499	-0.0374	-0.02644	-0.14858	0.204392	0.146905	0.384932	0.096039	0.166064	0.010915	0.314255
-0.00068	0.1108	0.025088	-0.23321	0.064336	0.008926	-0.20391	0.003098	0.131556	-0.18676	0.040729	-0.0428	-0.02145	-0.11505
0.087348	-0.16441	-0.13684	0.197766	-0.17156	0.149599	0.102825	-0.11711	-0.22177	0.007009	-0.13237	-0.26626	-0.24662	-0.1585
-0.02457	-0.25556	-0.14597	-0.11979	-0.00536	0.031776	0.307169	0.004337	-0.19921	0.022263	-0.28917	-0.04962	-0.0697	0.157511
-0.06073	-0.08936	-0.07982	0.037568	-0.23054	0.254568	0.218286	-0.18155	-0.20673	-0.01361	-0.27899	-0.16778	-0.20909	-0.14072
0.055957	-0.16441	-0.04447	0.017721	-0.27343	-0.00464	0.065791	-0.18403	-0.22177	0.293957	-0.24641	-0.06249	0.010723	0.036045

-0.10213	-0.06962	-0.09403	-0.06852	-0.10127	-0.09208	-0.0463	-0.15005	-0.08926	0.053615	-0.13506	-0.06604	-0.0463	-0.0463
-0.06588	0.370178	0.112644	-0.02652	-0.06533	0.110308	-0.02987	-0.09679	-0.05758	-0.06917	-0.08712	-0.0426	-0.02987	-0.02987
-0.06077	-0.06025	0.023976	-0.0897	-0.06025	-0.05479	-0.02755	-0.08928	-0.05311	0.191403	0.175329	-0.03929	-0.02755	-0.02755
-0.04552	0.315948	0.029934	-0.06719	-0.04514	-0.04104	-0.02064	-0.06688	-0.03978	-0.04779	-0.02736	-0.02943	-0.02064	-0.02064
-0.03739	-0.03707	0.26061	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	-0.03925	0.085398	-0.02418	-0.01695	-0.01695
-0.12064	-0.08895	-0.08665	-0.07845	-0.11962	-0.10876	-0.05469	-0.11828	-0.10543	0.029229	-0.0145	-0.07801	-0.05469	-0.05469
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	0.431788	0.355075	-0.02418	-0.01695	-0.01695
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	0.431788	0.355075	-0.02418	-0.01695	-0.01695
0.097042	-0.07358	-0.06832	-0.10954	-0.07358	-0.0669	-0.03364	0.108567	-0.06485	0.209761	0.148913	-0.04798	-0.03364	-0.03364
0.022761	-0.04514	-0.04191	-0.06719	-0.04514	-0.04104	-0.02064	0.019882	-0.03978	0.52572	0.432319	-0.02943	-0.02064	-0.02064
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	-0.03925	-0.04944	-0.02418	-0.01695	-0.01695
-0.04643	-0.04604	-0.04274	-0.06853	-0.04604	-0.04186	-0.02105	-0.06821	-0.04058	-0.04875	-0.0614	-0.03002	-0.02105	-0.02105
-0.03739	-0.03707	-0.03442	-0.05519	-0.03707	-0.03371	-0.01695	-0.05493	-0.03268	-0.03925	-0.04944	-0.02418	-0.01695	-0.01695
-0.05333	-0.05288	-0.0491	-0.07871	-0.05288	-0.04808	-0.02418	0.429839	0.128167	0.279946	0.217971	-0.03448	-0.02418	-0.02418
-0.03739	-0.03707	0.703155	-0.05519	-0.03707	-0.03371	-0.01695	0.568567	-0.03268	-0.03925	-0.04944	-0.02418	-0.01695	-0.01695
0.056316	0.071615	0.203341	0.013999	0.136096	0.035534	0.222176	0.327735	-0.05055	0.120575	0.326723	0.000179	-0.01869	-0.17676
-0.14717	0.07673	-0.02944	-0.02826	0.015072	-0.0929	-0.109	-0.05498	-0.04348	-0.27682	-0.12559	-0.03753	0.078934	0.146591
-0.1223	-0.0137	-0.08506	-0.18135	-0.15757	-0.10145	-0.10149	0.059588	-0.06159	0.147987	0.185397	-0.04289	-0.03383	-0.15411
0.068404	-0.02466	0.125403	-0.13907	-0.20416	-0.07582	-0.10149	-0.12148	0.059781	-0.07138	-0.03588	0.262704	0.199214	0.154109
-0.17827	-0.15072	0.013086	0.010903	-0.04111	0.156974	-0.09397	0.098435	-0.01087	0.019151	0.009968	0.010723	-0.109	0.206731
0.30471	0.054807	0.007633	-0.06386	0.104134	-0.0267	-0.09397	0.106995	0.067028	0.078346	0.158484	-0.03217	-0.16914	-0.08645

0.185982	-0.0463	-0.0463	-0.12137	-0.1031	0.025572	1							
-0.12321	-0.02987	-0.02987	0.162612	-0.0665	-0.04862	-0.08159	1						
-0.11365	-0.02755	-0.02755	0.149987	-0.06134	-0.04484	-0.07526	-0.04855	1					
0.291244	-0.02064	-0.02064	-0.0541	-0.04595	0.196757	0.028187	-0.03636	0.033541	1				
-0.06992	-0.01695	-0.01695	-0.04443	-0.03774	-0.02759	-0.0463	-0.02987	0.247936	0.227	1			
0.084949	-0.05469	-0.05469	-0.00763	-0.12178	0.224035	-0.08476	-0.09637	0.389754	-0.0461	0.029449	1		
-0.06992	-0.01695	-0.01695	0.365699	-0.03774	-0.02759	-0.0463	-0.02987	0.523421	-0.02064	-0.01695	0.281865	1	
-0.06992	-0.01695	-0.01695	0.365699	-0.03774	-0.02759	-0.0463	-0.02987	0.523421	-0.02064	-0.01695	0.281865	1	1
-0.13878	-0.03364	-0.03364	-0.08819	-0.07491	-0.05476	-0.0919	-0.05928	0.323868	-0.04096	-0.03364	0.353914	-0.03364	-0.03364
-0.08513	-0.02064	-0.02064	0.345385	-0.04595	-0.03359	-0.05637	-0.03636	0.503122	-0.02513	-0.02064	0.261229	0.969907	0.969907
-0.06992	-0.01695	-0.01695	-0.04443	-0.03774	-0.02759	-0.0463	-0.02987	-0.02755	-0.02064	-0.01695	0.450143	-0.01695	-0.01695
-0.08683	-0.02105	-0.02105	-0.05517	-0.04687	-0.03426	-0.0575	-0.03709	-0.03421	-0.02563	-0.02105	0.071398	-0.02105	-0.02105
-0.06992	-0.01695	-0.01695	-0.04443	-0.03774	-0.02759	0.474583	-0.02987	-0.02755	-0.02064	-0.01695	-0.05469	-0.01695	-0.01695
-0.09973	-0.02418	-0.02418	0.375369	0.592134	-0.03935	-0.06604	-0.0426	-0.03929	-0.02943	-0.02418	-0.07801	-0.02418	-0.02418
-0.06992	-0.01695	-0.01695	0.160634	0.641578	-0.02759	-0.0463	-0.02987	-0.02755	-0.02064	-0.01695	-0.05469	-0.01695	-0.01695
-0.3288	-0.16924	-0.20687	0.290993	0.376548	0.093852	-0.3505	-0.03736	0.253046	0.063389	-0.05633	0.00383	0.18454	0.18454
-0.12813	0.191696	0.101486	-0.03866	-0.01674	-0.22989	-0.23616	0.050781	0.089603	-0.06315	-0.03383	-0.1216	-0.04886	-0.04886
0.223209	-0.07893	-0.09397	0.178116	0.123031	0.097024	0.261833	0.046365	0.026474	0.083291	-0.12404	0.176329	0.139074	0.139074
0.155879	0.071416	-0.16914	-0.04017	-0.04603	0.095276	0.211135	-0.04637	-0.03462	0.105258	0.056381	0.290772	-0.109	-0.109
0.137516	-0.05638	-0.00376	-0.0144	0.117172	-0.05157	0.27916	-0.08169	-0.02036	-0.05034	0.199214	0.077436	0.048864	0.048864
-0.11466	0.093969	-0.18418	0.161442	0.189149	0.037586	0.002567	0.22741	-0.0224	-0.1437	-0.03383	0.157048	0.161626	0.161626

Impatiens balsamifera	*Valeriana officinalis*	*Silene diocia*	*Cirriphylum piliferum*	*D. Flexuosa*	*Mercurialis perennis*	*C. oppositi-folium*	organic content	moisture content	air temperature	soil temperature	illumination	P.A.R.
1												
0.110276	1											
0.587427	-0.02064	1										
0.129613	-0.02563	0.259589	1									
-0.03364	-0.02064	-0.01695	-0.02105	1								
-0.04798	-0.02943	-0.02418	-0.03002	-0.02418	1							
-0.03364	-0.02064	-0.01695	-0.02105	-0.01695	-0.02418	1						
0.059435	0.18986	-0.04127	0.014177	-0.14665	0.26322	0.161959	1					
-0.1693	-0.09061	-0.18418	0.018152	-0.14659	-0.1662	0.063899	-0.02579	1				
0.153227	0.152853	0.199214	0.254648	0.078934	0.048252	0.093969	0.013605	-0.15588	1			
0.203729	-0.07597	0.176661	0.045121	0.146591	-2.10E-18	-0.01128	-0.36209	-0.25374	0.306696	1		
0.020086	0.054002	0.109004	-0.01711	0.184179	0.144755	0.146591	-0.20768	-0.20728	0.282745	0.267797	1	
0.093543	0.193126	0.109004	0.11358	0.101486	0.139394	0.003759	0.048214	-0.32626	0.258127	0.268575	0.238455	1